EARLY AND MIDDLE PERMIAN CONODONTS FROM THE CANNING AND SOUTHERN CARNARVON BASINS, WESTERN AUSTRALIA: THEIR IMPLICATIONS FOR REGIONAL BIOGEOGRAPHY AND PALAEOCLIMATOLOGY

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Small, low diversity conodont faunas have now been recovered from the Early to Middle Permian (Cisuralian–Sakmarian to Guadalupian–Capitanian) of Western Australia. These faunas negate earlier suggestions that there might be no conodonts in the cool water high palaeolatitude (up to 60°S) basins of the post-glacial Permian of the Southern Carnarvon and Canning Basins. Species of the genera *Hindeodus* and *Vjalovognathus* appear to be cool-temperature tolerant forms that were the first conodonts to invade these marine shelf environments after the Late Carboniferous–Early Permian glaciation. Faunas of similar age from Timor, at a palaeolatitude of about 45°S, show significantly greater faunal diversity.

Conodonts in the Southern Carnarvon Basin have been recovered from the Callytharra, Coyrie and Wandagee Formations and the Coolkilya Sandstone. The Callytharra Formation fauna consists of *Vjalovognathus australis* sp. nov. and *Hindeodus* sp. and correlates with the *Mesogondolella bisselli–Sweetognathus inornatus* Zone (Sakmarian to Artinskian). The Coyrie Formation contains *V. shindyensis* and *Hindeodus* sp. and is assigned to the *Mesogondolella idahoensis–Vjalovognathus shindyensis* Zone (Kungurian). The Wandagee Formation and the Coolkilya Sandstone contain only elements of *Vjalovognathus* sp. nov. A, for which a tentative assignment to the *Mesogondolella nankingensis* Zone can be made. Associated ammonites in the Coolkilya Sandstone indicate a Roadian (Ufimian) age for the upper limit of this taxa.

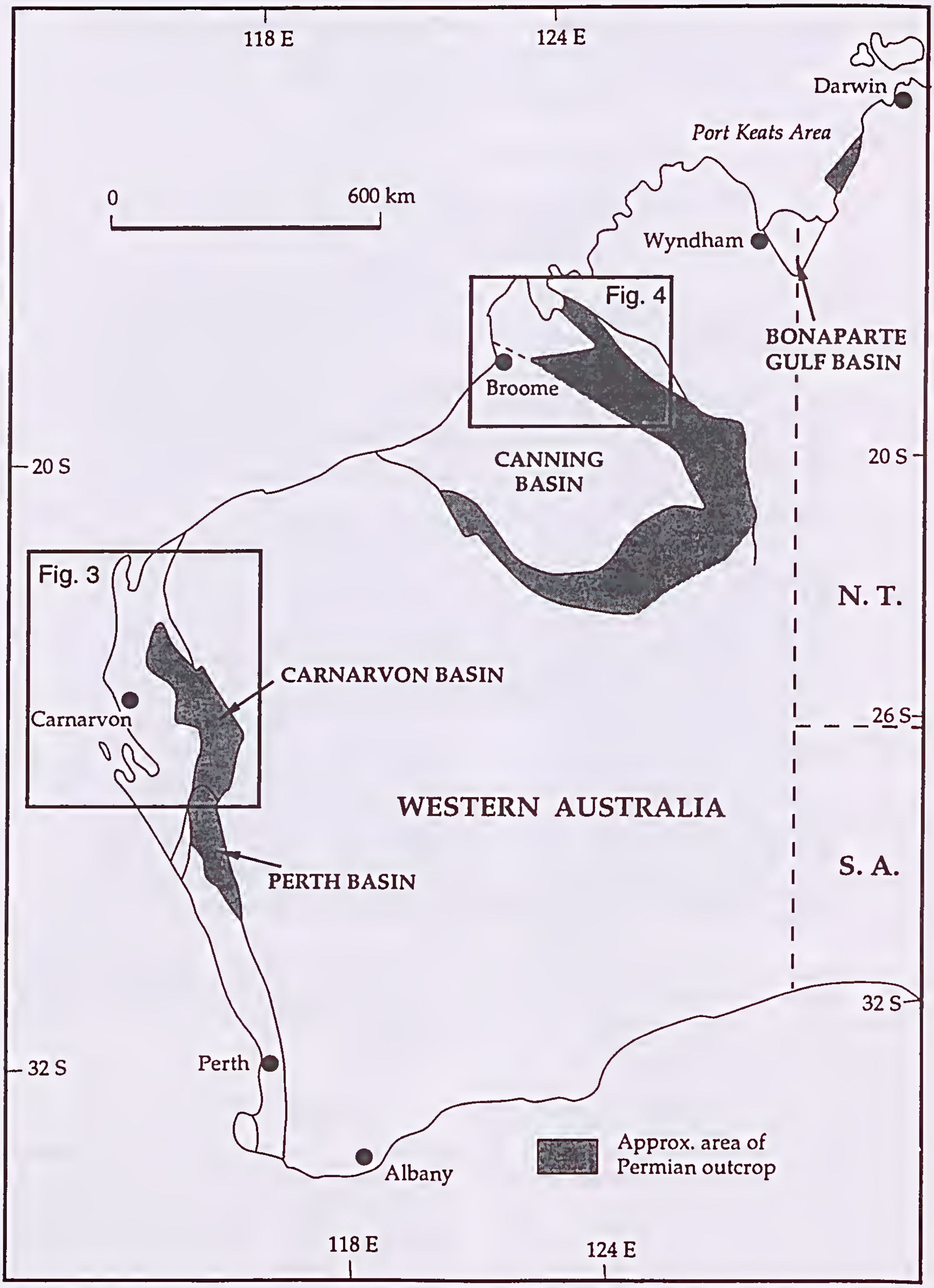
In the Canning Basin the conodont fauna found in the Noonkanbah Formation contains *Mesogondolella idahoensis*, *V. shindyensis* and *Hindeodus* sp. and is assigned to the *Mesogondolella idahoensis–Vjalovognathus shindyensis* Zone of Kungurian age.

The genus *Vjalovognathus* evolved from the general lineage of 'naked' gondolellids of the Late Pennsylvanian, from forms like *Gondolella postdenuda* von Bitter & Merrill, with the development of a scaphate aboral surface. *Vjalovognathus australis* from the late Sakmarian–Early Artinskian is the oldest recognised species of the genus. This species gave rise to *V. shindyensis* in the Kungurian and to *V.* sp. nov. A in the late Kungurian to Roadian (Ufimian). The youngest identified species of *Vjalovognathus* is found in faunas from the Chhidru Formation (Late Permian–Changhsingian) of the Salt Range of Pakistan.

THE apparent lack of conodonts in the marine Lower Permian of Western Australia (Fig. 1), despite extensive sampling, led Nicoll (1976) to conclude that the absence of conodonts in these sediments was due to the glacial-related lowered temperatures of marine water being below the tolerance level of the conodont animal. Subsequently, Nicoll (1984) reported a very limited, and at that time not specifically identified, Permian conodont fauna from the Noonkanbah Formation of the Canning Basin. Additional Permian conodont material has now been recovered from the Noonkanbah Formation and also from formations in the Southern Carnarvon Basin, Western Australia. We here report the first unequivoeal Permian conodonts from Australia and discuss their biostratigraphic, biogeographic and palaeoclimatological significance.

SOUTHERN CARNARVON BASIN

In 1974 one of us (R.S.N.) collected 308 samples from eight stratigraphic units of Permian age in the Southern Carnarvon Basin (Figs 2, 3; Appendix). Initially none of these samples was thought to contain conodonts (Nicoll, 1976), but a few supposed fish teeth were observed.


118 E
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Darwin
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BONAPARTE
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20 S
20 S
Fig. 3
N. T.
CARNARVON BASIN
Carnarvon
26 S
WESTERN AUSTRALIA
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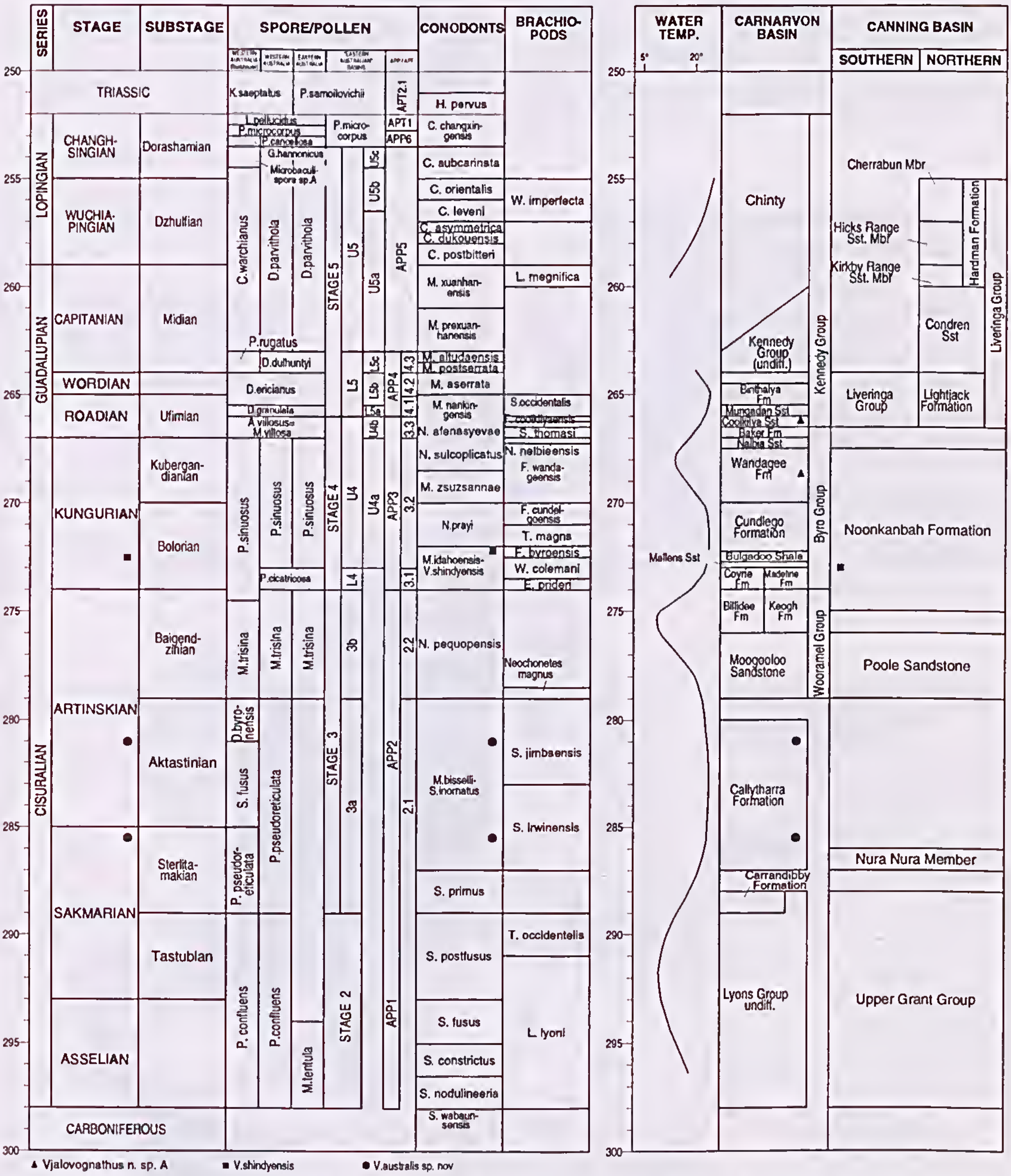


Fig. 2. Generalised stratigraphy of the Canning and Southern Carnarvon Basins, brachiopod zonation, conodont occurrences and water temperature curve for the Permian of Western Australia (modified after Archbold & Shi 1995).

Fig. 1. Map showing Permian outcrops in Western Australia and locations of the Canning and Southern Carnarvon Basins.

Following the publication by van den Boogaard (1987) of Permian conodonts from Timor, the 'fish teeth' were re-examined and found to be broken elements of the unusual scaphate conodont genus *Vjalovognathus* Kozur (1977). All of the conodont residues from the Nicoll (1974) sampling that could be located were re-examined for conodonts and a total of 114 elements, mostly fragments of *Vjalovognathus australis* sp. nov. along with six fragments of *Hindeodus* sp. elements, were

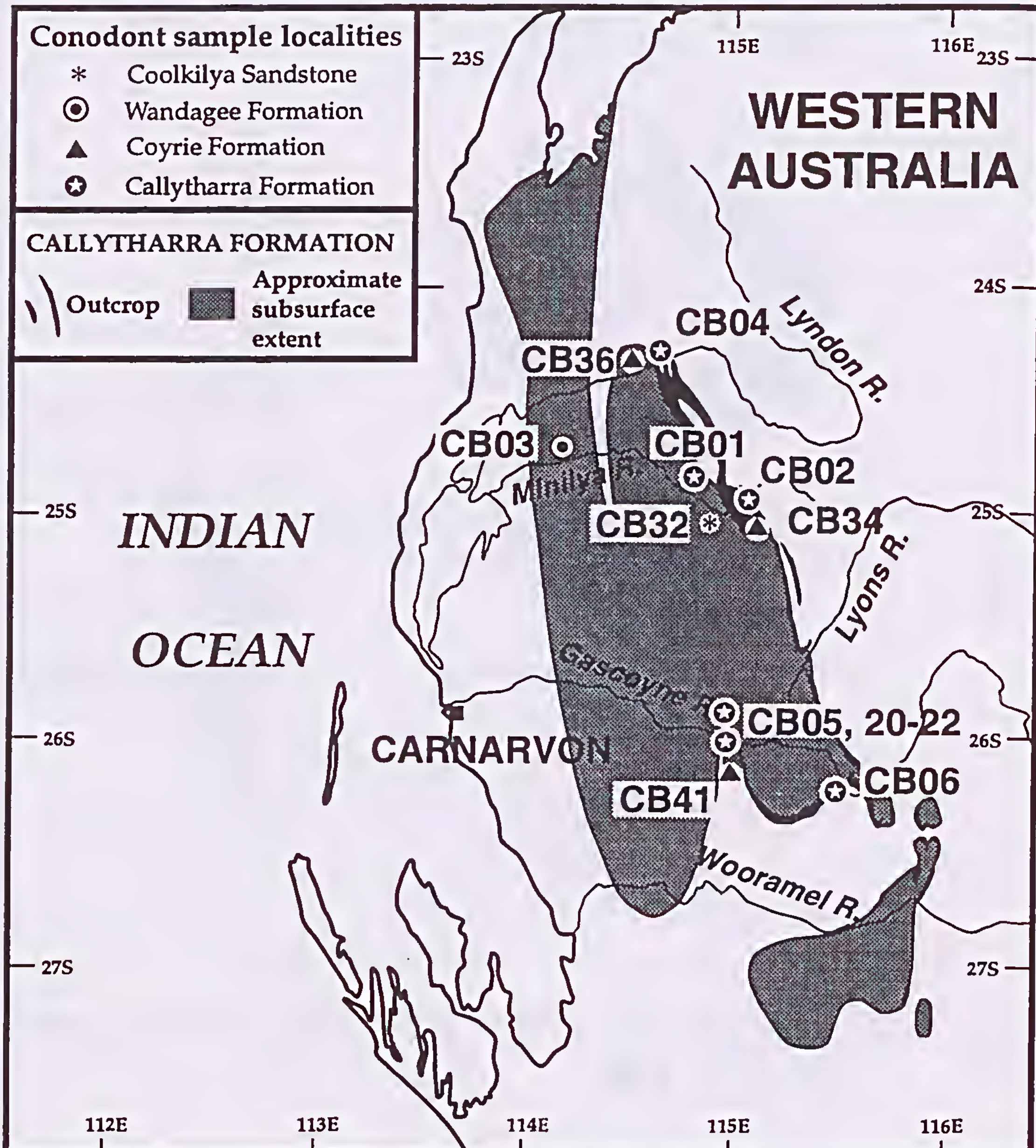


Fig. 3. Map showing the distribution of the Callytharra Formation and conodont sample localities in the Southern Carnarvon Basin.

recovered from 48 of 208 sample residues. One hundred sample residues from the 1974 collection, 87 of which were from Callytharra Formation section 04, could not be relocated. A total of 100 conodonts were obtained from 43 samples of the Callytharra Formation. Of the eight samples of the Coyrie Formation, three samples produced a total of six conodont elements. The seven samples of the Wandagee Formation yielded seven elements from one productive sample. One of the seven samples from the Coolkilya Formation produced a single conodont element.

Dr Arthur Mory (Geological Survey of Western Australia) has provided 11 additional samples of newly collected material from the Callytharra and Coyrie Formations and the Coolkilya Sandstone in an effort to provide additional material from some stratigraphic intervals where few conodont elements have been recovered. From these samples an additional four elements were recovered from 82 kg of samples processed.

Conodont productivity in the Permian of the Southern Carnarvon Basin is low. Slightly over 900 kg of samples processed from the initial collecting produced only 114 conodonts. That is about one conodont element for each 8 kg of rock processed. The additional Mory samples, mostly from localities known to contain conodonts, have produced four elements from 82 kg of rock processed.

CANNING BASIN

Samples were collected from the Lower Permian Noonkanbah Formation (Fig. 4) which comprises grey, micaceous, pyritic mudstone interbedded with fine to medium-grained, laminated and thin-bedded calcareous sandstones and minor finely crystalline fossiliferous limestone interbeds (Towner & Gibson 1983). Limestone interbeds from the middle part of the formation were collected for conodont extraction. A rich macrofauna, including brachiopods, bryozoans, corals, crinoids and molluscs, indicates an Artinskian to lower Kungurian age (Archbold 1993; Archbold & Shi 1995: fig. 2). The depositional environment is interpreted as unrestricted marine with shallower

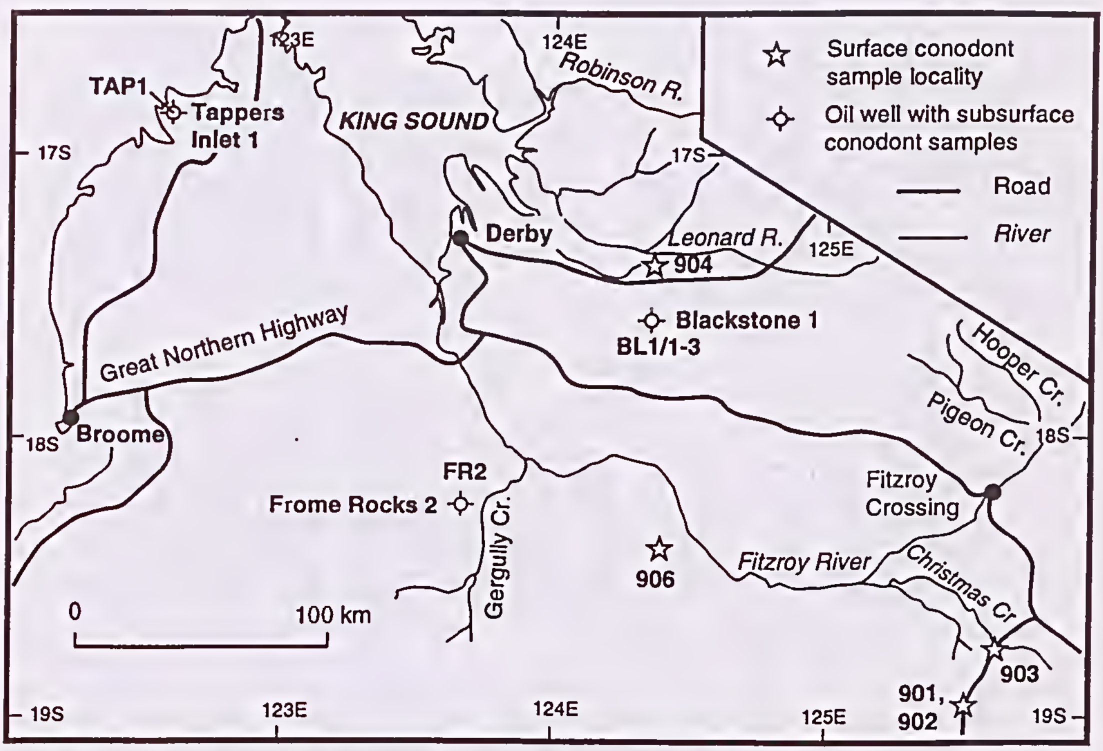


Fig. 4. Map showing locations of conodont samples in the Canning Basin.

Stage	Conodont Zones and Assemblage Zones		Conodont Standard Zonation	Conodont Zones (this study)
	Shallow-water	Pelagic		
Roadian	*Sweetognathus subsymmetricus* *Neostreptognathodus clinei*	*Mesogondolella nankingensis* (part)	*Mesogondolella nankingensis*-*Sweetognathus subsymmetricus*	*M. nankingensis* *
Cathedralian	*N. sulcoplicatus*	*Mesogondolella idahoensis*	*M. idahoensis*-*N. sulcoplicatus*	*N. sulcoplicatus*
	Sichuanognathus ? prayi	*Mesogondolella zsuzsanne*	*M. zsuzsanne*-*S. ? prayi*	*M. zsuzsanne*
		M. idahoensis-*M. asiaticai*	*M. idahoensis*-*S. ? prayi*	*N. prayi*
	N. exsculptus-*N. pnevi*	*V. shindyensis*-*M. intermedia*	*M. idahoensis*-*N. exsculptus*	*M. idahoensis*-*V. shindyensis* *
			M. intermedia-*N. exsculptus*	
Artinskian	*N. pequopensis*-*N. ruzhhencivi*	*Mesogondolella bisselli*	*M. bisselli*-*N. pequopensis*	*N. pequopensis*
	Sweetognathus whitei		*M. bisselli*-*S. whitei*	*M. bisselli*-*S. inornatus* *
	S. inornatus-*S. whitei*		*M. bisselli*-*S. inornatus*	
Sakmarian	*S. inornatus*-*S.* n. sp.	*M. bisselli*-*M. visiibilis*	*M. bisselli*-*M. visiibilis*	
	Sweetognathus merrilli	*M. obliquimarginata*	*M. obliquimarginata*-*S. merrilli*	NO DATA
Asselian	*Wardlawella expansa*-*Streptognathodus postfusus*	*Mesogondolella adentata*-*Streptognathodus postfusus*	*Streptognathodus postfusus*	
	Wardlawella expansa-*Streptognathodus constrictus*	*Mesogondolella adentata*-*Streptognathodus constrictus*	*Streptognathodus constrictus*	
	Wardlawella expansa-*Streptognathodus barskovi*	*Streptognathodus barskovi*-*Streptognathodus invaginatus*	*Streptognathodus barskovi*-*Streptognathodus invaginatus*	

Fig. 5. Shallow-water, pelagic and 'standard' Lower Permian conodont zones of Kozur (1995).

conditions in some areas. A thickness of 410 m was recorded for the Noonkanbah Formation in the Sisters 1 well (Forman & Wales 1981).

Thirteen samples from the Noonkanbah Formation have yielded conodonts out of a total 16 samples collected weighing a total 220 kg of rock. Eight of these (samples 901/2, 902/1, 902/2A, 903/1, 904/1, 906/1, 906/5 and 906/6), are surface outcrop samples from the Bruten, Meda and Nerrima areas and five are from subsurface samples from the Frome Rocks 2 (FR2, core 2, 1099–1109 ft depth), Tappers Inlet 1 (TAP1, core 3, 2850–2900 ft depth) and Blackstone 1 (BL1/1, 420–450 ft depth; BL1/2, 510–540 ft depth; and BL1/3, 540–570 ft depth) wells (Fig. 4).

Faunas from the Noonkanbah Formation of the Canning Basin include *Mesogondolella idahoensis* (Youngquist, Hawley & Miller) and *Vjalovognathus shindyensis* (Kozur) which suggests a Kungurian age for this formation at the sampled localities and this is in accord with the previously assigned age based on other palaeontological evidence (Archbold 1993, 1998; Archbold & Shi 1995).

BIOSTRATIGRAPHY

A recent summary of Australian Permian biostratigraphy has been presented by Archbold & Dickins (1996) who discussed the interrelationship of biostratigraphic schemes based on ammonoids, bivalves, brachiopods, floras and palynomorphs. Archbold (1998) has recently reviewed and updated the Permian biostratigraphy of the Western Australian basins. The geology and stratigraphy of the Canning and Southern Carnarvon Basins (Fig. 1) has been described by Towner & Gibson (1983), Yeates et al. (1984), Hocking et al. (1987), Goldstein (1989) and Mory & Backhouse (1997). Summary stratigraphies for the Permian of the Canning and Southern Carnarvon Basins are given in Fig. 2. A brachiopod zonation for Western Australia has recently been proposed by Archbold (1993) and relationships of this zonation to Asian faunas and Permian climate are discussed by Archbold & Shi (1995) who have constructed a water temperature curve for the shallow marine Permian of Western Australia (Fig. 2).

Conodont faunas representing three zones are now recognised in the Canning and Southern Carnarvon Basins and in Timor (Figs 2, 5). The oldest of these is the *Mesogondolella bisselli–Sweetognathus inornatus* Zone. The middle is the *Mesogondolella idahoensis–Vjalovognathus shindyensis* Zone and the youngest is tentatively assigned to the *Mesogondolella nankingensis* Zone. A single undescribed juvenile conodont element, possibly of late Middle Permian (Late Capitanian) age, has been recovered (see below). The three conodont faunas from the Southern Carnarvon and Canning Basins, together with the fauna earlier described from Timor by van den Boogaard (1987), provide valuable correlation control points for the Lower and Middle Permian of Western Australia in terms of the international Permian stage terminology (Jin et al. 1997). Identification of zonal indicators in both the Sakmarian–Artinskian (*Mesogondolella bisselli–Sweetognathus inornatus* Zone) and Kungurian (*Mesogondolella idahoensis–Vjalovognathus shindyensis* Zone) faunas provide important correlation between Australia, Timor and the Tethys region. Timor ammonoid and brachiopod faunas provide additional biostratigraphic ties (Furnish & Glenister 1971; Furnish 1973; van den Boogaard 1987; Archbold & Barkham 1989; Archbold & Bird 1989).

Mesogondolella bisselli–Sweetognathus inornatus Zone

The *Mesogondolella bisselli–Sweetognathus inornatus* Zone is essentially equivalent to the *Mesogondolella bisselli–Sweetognathus whitei* Zone of Ritter (1986) and the *Sweetognathus inornatus–S. whitei* through *Sweetognathus whitei* Zones or the *Mesogondolella bisselli–M. visibilis* through *M. bisselli–S. whitei* Zones of Kozur (1995) (Fig. 6). The base of the zone is marked by the first appearance of *Mesogondolella bisselli* and *Sweetognathus whitei* and the co-occurrence of *M. bisselli* and *S. inornatus. Vjalovognathus australis* occurs within the zone, but the level of the earliest occurrence of this species has not been documented. The upper limit of the zone is marked by the first appearance of *Neostreptognathodus pequopensis.* The zone ranges in age from the upper Sakmarian (Sterlitamakian) through the early Artinskian (Aktastinian) based on the age of associated ammonoids in the Timor localities.

The *Mesogondolella bisselli–Sweetognathus inornatus* Zone is now known from the Callytharra Formation of the Southern Carnarvon Basin and from the Maubisse Formation in West Timor (van den Boogaard 1987; Barkham 1993). Conodont elements recovered from the Callytharra Formation are mostly Pa elements of *Vjalovognathus australis* sp. nov. along with a few broken Pa elements of *Hindeodus* which cannot be specifically identified.

Stage	Conodont Zones (this study)	Conodont Standard Zonation (Kozur, 1994)	Eastern Gondwana Province Conodont Zones (Kozur, 1994)		
			Shallow-water	Pelagic	Standard
Roadian (Ufimian)	*M. nankingensis* *		unknown	unknown	unknown
Kungurian (Cathedralian)	*N. sulcoplicatus*	*M. idahoensis-N. sulcoplicatus*			
	M. zsuzsanne	*M. zsuzsanne-N. prayi*			
	N. prayi	*M. idahoensis-N. prayi*	*N. leonovae*	*M. idahoensis*	*M. idahoensis-N. leonovae*
	M. idahoensis-V. shindyensis *	*M. idahoensis-N. exsculptus*			
		M. intermedia-N. exsculptus	*N. exsculptus-R. bucaramangus*	*M. intermedia-V. shindyensis*	*N. exsculptus-V. shindyensis*
Artinskian	*N. pequopensis*	*M. bisselli-N. pequopensis*	unknown	*M. bisselli-V. shindyensis*	*M. bisselli-V. shindyensis*
Sakmarian	*M. bisselli-S. inornatus* *	*M. bisselli-S. whitei*			

Fig. 6. Correlation of standard and Eastern Gondwana province conodont zones (from Kozur 1994).

In West Timor the *Mesogondolella bisselli–Sweetognathus inornatus* Zone has been documented from the Maubisse Formation in two regions, the Bitauni–Bisnain area and SW Mutis area (this study; van den Boogaard 1987). Cephalopod-bearing grey limestones and marls from the Maubisse Formation (Kekneno Series) of the SW Mutis region yield '*Vjalovognathus shindyensis*' (here reinterpreted as *Vjalovognathus australis*, see below) together with *Mesogondolella bisselli* Clark & Behnken, *Sweetognathus* aff. *whitei* Rhodes (=*S. inornatus* Ritter, 1986) and *Sweetocristatus* sp. Ammonoids from these Mutis sediments indicate a Sakmarian age (van den Boogaard 1987).

Conodont faunas from cephalopod-bearing marls in the Bitauni area include *Vjalovognathus australis* together with *Mesogondolella bisselli* (Clark & Behnken, 1971), *Diplognathus oertlii* Kozur, 1975, *Neospathodus* cf. *praedivergens* (Kozur & Mostler, 1976), *Sweetognathus* cf. *behnkeni* Kozur, 1975, *Sweetognathus* aff. *whitei* (Rhodes, 1963 = *S. inornatus* Ritter, 1986) and *Sweetocristatus* sp. (van den Boogaard, 1987). Conodonts from a new sample (Barkham 1993, sample SB18) of the Maubisse Formation from the Bisnain River near Bisnain contain additional specimens of *V. australis* (Fig. 11C–H). The ammonoids from which the van den Boogaard (1987) conodont samples were obtained indicate an Artinskian age.

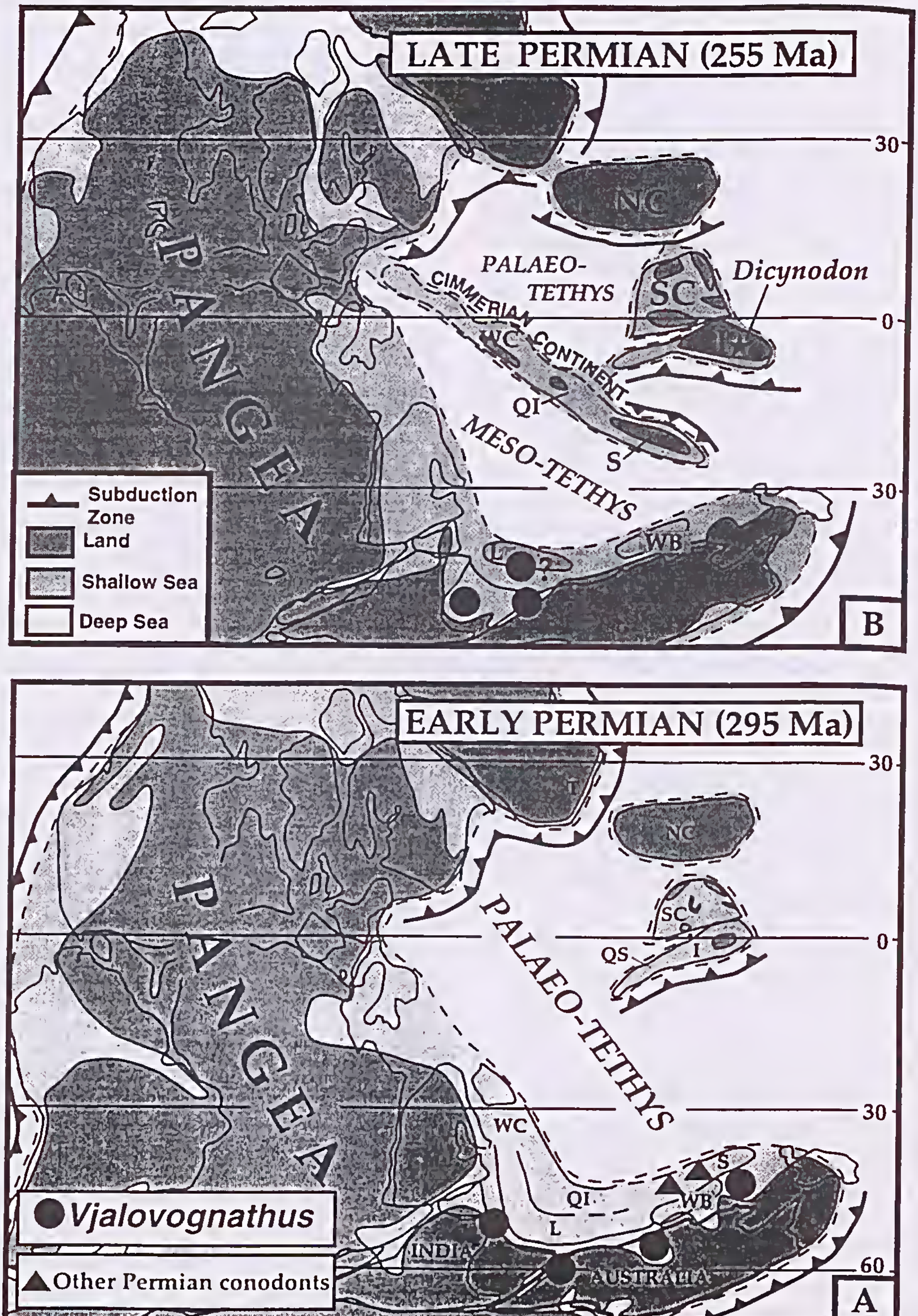
Reimers (1991) also discusses an association of '*Neogondolella*' *bisselli* and *Vjalovognathus shindyensis* in the sections of the Lower Kotchusuy Suite, supposedly of Bolorian age, in the south-eastern Pamir. Both of the illustrated specimens of *V. shindyensis* (Reimers 1991: pl. 1, figs 9, 12, 14) appear to be specimens of *V. australis*. This association of *Mesogondolella bisselli*, *Sweetognathus inornatus* and *V. australis* in the lower part of the Kotchusuy Suite means that the lower part of this interval is Artinskian in age and not Bolorian (Kungurian) as previously interpreted.

Mesogondolella idahoensis–Vjalovognathus shindyensis Zone

The Mesogondolella idahoensis–Vjalovognathus shindyensis Zone is defined by the co-occurrence of *Mesogondolella idahoensis* and *Vjalovognathus shindyensis*. The *Mesogondolella idahoensis–Vjalovognathus shindyensis* Zone is possibly found in the Coyrie Formation of the Southern Carnarvon Basin and in the middle part of the Noonkanbah Formation in the Canning Basin.

In reviewing the literature relating to the stratigraphic distribution of *Vjalovognathus shindyensis* it has become apparent that the working definition of the species has been very loose; that there are multiple species of the genus that have not been differentiated; and as a result, the identification of *V. shindyensis* in various studies may well be incorrect and the stratigraphic range of conodonts and associated faunas may not make sense. *Vjalovognathus shindyensis* was first described as '*Vjalovites*' *shindyensis* by Kozur & Mostler (1976) from the upper Leonardian Grenze des Chihsian at Shindy in the Pamirs. The type specimen of *V. shindyensis* from the Shindi River exposure of the Buz Tere Complex in the Pamirs (Kozur & Mostler 1976) has oral surface denticles that conform with the material that we illustrate herein as *V. shindyensis*. However, both van den Boogaard (1987: fig. 8) and Kozur (1995: pl. 4, fig. 1) illustrated Timor specimens as *V. shindyensis* that we here differentiate on the basis of oral surface denticle morphology and name as *V. australis*. Because the Timor material is late Sakmarian to early Artinskian (see above), we suggest that other non-illustrated references to the identification of *V. shindyensis* may also be suspect, especially when associated with *Mesogondolella bisselli* (e.g. Reimers 1991). We here suggest that *V. shindyensis* ss. is probably mostly of earliest Kungurian (Bolorian) age, especially when it is associated with *M. idahoensis* and *Neostreptognathodus leonovae*.

Faunas from the Noonkanbah Formation of the Canning Basin include *Hindeodus* sp., *Mesogondolella idahoensis* (Youngquist, Hawley & Miller) and *Vjalovognathus shindyensis* (Kozur). *Mesogondolella idahoensis* was first described from the Phosphoria Formation in southern Idaho (Youngquist et al. 1951) and is generally considered to be a late Artinskian (Leonardian) species in North America (Clark & Behnken 1971; Behnken 1975; Sweet 1988). It occurs in the *Neostreptognathodus leonovae* and *Neostreptognathodus clinei–Mesogondolella nankingensis* Zones of Middle–Upper Leonardian–Chihsian age (Kozur 1978). In China, *Mesogondolella idahoensis* occurs in the early Chihsian, which is equated with the late Artinskian (Leonardian) of North America. In Japan, *Mesogondolella idahoensis* occurs in the late Sakamotozawan to early Nabeyaman which is broadly equivalent to the Leonardian of North America. Kozur (1994, 1995) has proposed a new scheme of conodont zones for the Lower Permian, including Shallow-water, Pelagic and 'Standard' zones (Fig. 5). In this scheme, the Noonkanbah conodont faunas would represent the early Cathedralian (Kungurian) *Mesogondolella intermedia–Neostreptognathodus exculptus* and


LATE PERMIAN (255 Ma)
30
NC
PALAEO-
TETHYS
CIMMERIAN CONTINENT
SC
Dicynodon
0
QI
MESO-TETHYS
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30
WB
L
B
Subduction Zone
Land
Shallow Sea
Deep Sea
PANGEA
EARLY PERMIAN (295 Ma)
30
NC
SC
QS
I
0
PALAEO-TETHYS
PANGEA
WC
30
S
WB
QI
L
INDIA
AUSTRALIA
60
A
Vjalovognathus
Other Permian conodonts

M. idahoensis–N. exculptus Standard Conodont Zones. Kozur (1994, 1995) also proposed preliminary Shallow-water, Pelagic and 'Standard' conodont zones representative of an Eastern Gondwana Province (Fig. 6). In this scheme, the Noonkanbah Formation faunas would represent the *N. exculptus–V. shindyensis* and the lower part of the *M. idahoensis–M. leonovae* Eastern Gondwanan Standard Zones. The presence of *Mesogondolella idahoensis* in the faunas from the Canning Basin suggests a Leonardian (Kungurian) age for the Noonkanbah Formation at the sampled sites which appear to be near the middle part of the formation.

Mesogondolella nankingensis Zone?

In Australia the only Permian conodonts thus far recovered, with one exception, from above the level of the *Mesogondolella idahoensis–Vjalovognathus shindyensis* Zone are elements of a new species of *Vjalovognathus*. *Vjalovognathus* sp. nov. A has characteristics that place it between *V. shindyensis* and the undescribed *Vjalovognathus* specimens reported by Wardlaw & Pogue (1995) from the upper part of the Chhidru Formation (Late Changhsingian) of Pakistan.

The *Mesogondolella nankingensis* Zone is tentatively interpreted to be represented by the presence of *Vjalovognathus* sp. nov. A in the Coolkilya Sandstone and possibly in the Wandagee Formation. This zonal assignment is based on the identification in the Coolkilya Sandstone of the Ufimian (Roadian) ammonite *Daubichites goochi* (Teichert, 1942) (Glenister et al. 1993) which equates to the *Mesogondolella nankingensis* Zone (Jin et al. 1997).

Younger conodont faunas

A single undescribed juvenile Pa element of unknown generic affinity has been recovered from the Northern Carnarvon Basin in the WMC Fennel 1 well (core 4, 1559.9 m). This core is associated with a *D. ericianus* Zone (Lower Stage 5c) palynoflora (Gorter 1998, pers. comm.; Mory & Backhouse 1997) which is tentatively equated with the late Middle Permian (Guadalupian, late Capitanian). No conodont zonal information can be obtained from this occurrence, but it does indicate that an intensive examination of later Permian strata might produce useful conodont faunas. Future searches for conodonts in the Lightjack and Hardman Formations of the Canning Basin and the Hyland Bay Formation of the Bonaparte Basin, which formed in warm temperate to subtropical conditions, may prove fruitful.

BIOGEOGRAPHY AND PALAEOCLIMATOLOGY: DISTRIBUTION AND ECOLOGY OF THE GENUS *VJALOVOGNATHUS*

Biogeographically, *Vjalovognathus* appears to be restricted to the northern margin of eastern Gondwanaland (Fig. 7) and may help define an Eastern Gondwanaland Conodont Province as provisionally suggested by Kozur (1994). Specimens of the genus *Vjalovognathus* have been reported from the Pamirs (Kozur & Mostler 1976; Reimers 1991), the Salt Range of Pakistan (Wardlaw & Pogue 1995), the Selong section of Tibet (Wang 1997, pers. comm.), Timor (van den Boogaard 1987) and Western Australia (this study). The Sakmarian–early Artinskian species *V. australis* is known from the Carnarvon Basin, Timor and the Pamirs. The Kungurian species, *V. shindyensis* is known from the Canning and Southern Carnarvon Basins and the Pamirs. The Roadian species, *V.* sp. nov. A, is known only from the Southern Carnarvon Basin and the undescribed Changhsingian species is known only from the Salt Range.

All of the *Vjalovognathus* localities were located at 40°+S palaeolatitudes and in basins on shelves, or adjacent to, the Palaeo-Tethys or Meso-Tethys Oceans. Except for two of van den Boogaard's (1987) Timor localities and one Canning Basin sample, *Vjalovognathus* elements occur in low abundance (less than 10 specimens per sample) and conodont faunal diversity is generally low (less than five species). Only in the two northernmost localities of Timor and the Pamir are there more than five species present in any given sample (Table 1).

Fig. 7. Palaeogeographic reconstructions for the eastern Gondwanaland and Tethys region in the Early Permian (a) and Late Permian (b) showing the known distribution of the genus *Vjalovognathus* and other peri-Gondwanan conodont faunas. NC = North China; SC = South China; T = Tarim; I = Indochina; QS = Qamdao-Simao; WC = Western Cimmerian Continent; QI = Qiangtang; L = Lhasa; S = Sibumasu; WB = West Burma. After Metcalfe (1998).

Stage	Locality	Palaeolatitude	No. of species
Changhsingian	Salt Range	50S	4
Roadian	Carnarvon Basin	50S	1
Kungurian	Pamirs	45–50S	?
	Canning Basin	50S	3
	Carnarvon Basin	60S	1
Lower Artinskian	Timor	45S	8
to Upper	Pamirs	50S	8–9
Sakmarian	Carnarvon Basin	60S	2

Table 1. Palaeolatitudes and diversity (No. of species) of Eastern Gondwanaland Permian conodont faunas that include the genus *Vjalovognathus*.

It is here suggested that *Vjalovognathus* may have been tolerant to cool temperate conditions which allowed it to invade the immediate post-glacial marine environment of Western Australia. Archbold & Shi (1995) have proposed a water temperature curve for the Permian of Western Australia based on brachiopod assemblages and $\delta^{18}O$ data (Fig. 2). The occurrences of conodonts in the Callytharra, Coyrie and Noonkanbah Formations of the Southern Carnarvon and Canning Basins correspond to warm temperate peaks on the curve that immediately follow cold/cool temperate conditions (Fig. 2).

SYSTEMATIC PALAEONTOLOGY—TAXONOMIC NOTES

The sparse nature of most of the conodont taxa recovered in this study allows little scope for detailed systematic comment. For species of the genera *Hindeodus* and *Mesogondolella* we offer only some brief observations of the

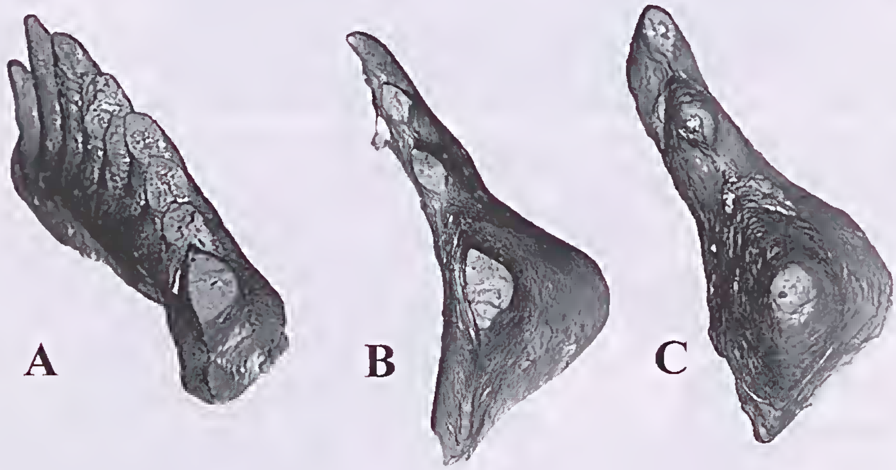
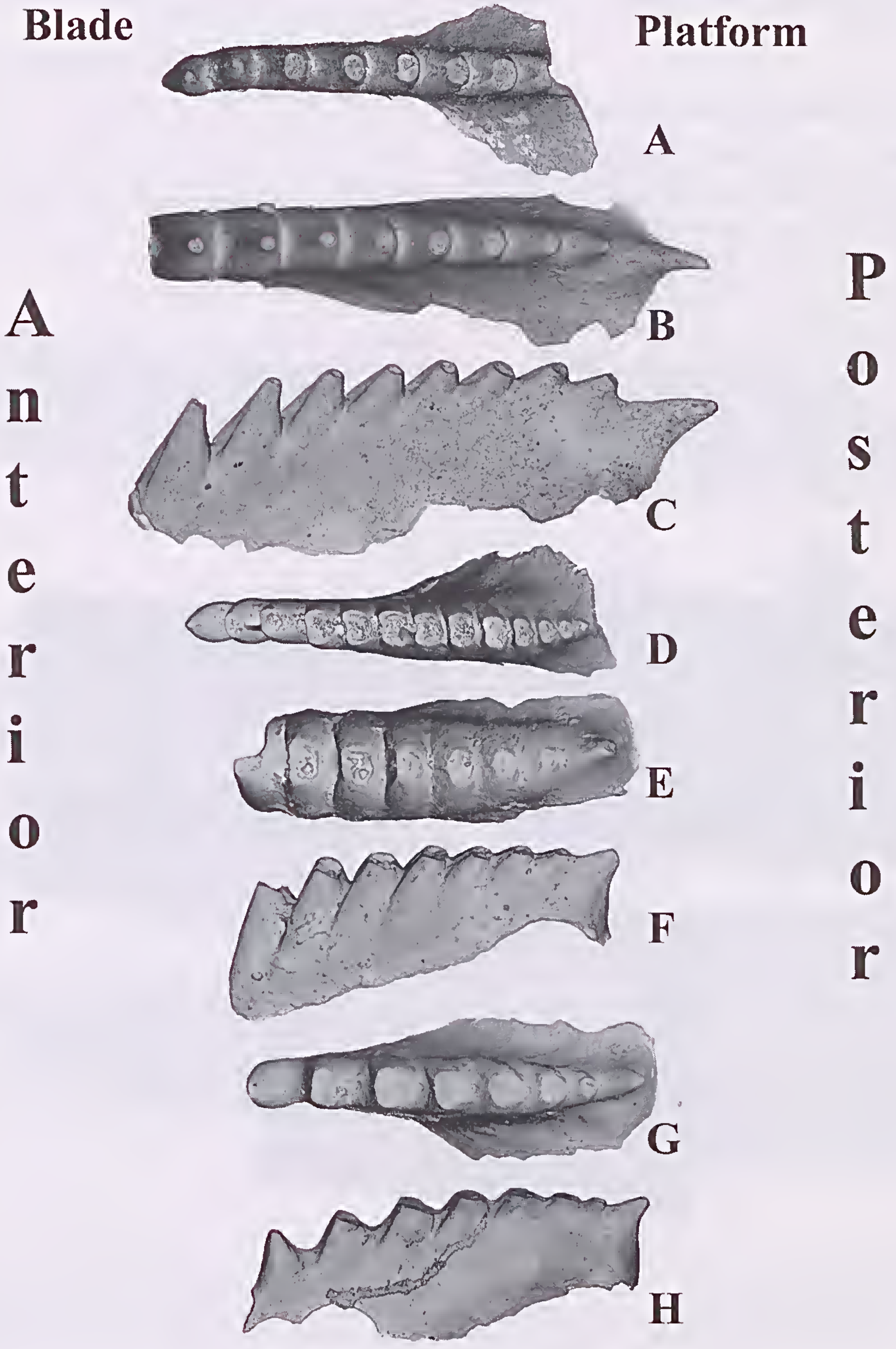


Fig. 8. Comparison of the oral views of the Pb elements of (A) *Mesogondolella idahoensis* (×170), (B) *Vjalovognathus shindyensis* (×150) and (C) *V. australis* (×130). Note the basic similarity of the dominant anterior process, cusp cross-section and outer lateral flare of the basal outline adjacent to the cusp. See following figures for specimen details.

Fig. 9. Morphology of the Pa element of *Vjalovognathus* Kozur, 1977 and comparison of the Pa elements of *V. australis* (A–C), *V. shindyensis* (D–F) and *V.* sp. nov. A (G–H). The blade is best preserved on the specimens A and D, and is broken on the other material. Anterior is to the left and the posterior with the cusp is to the right. The arrows mark the separation of blade from platform based on the outward flare of the basal margin. Note the change in denticle morphology between species and along each element. A, *V. australis* (CPC 34670) oral view (×75). B–C, *V. australis* (CPC 34644): B, oral view (×155); C, inner lateral view (×155). D, *V. shindyensis* (CPC 34678) oral view (×70). E–F, *V. shindyensis* (CPC 34679): E, oral view (×125); F, outer lateral view (×125). G–H, *V.* sp. nov. A (CPC 34693): G, oral view (×100); H, outer lateral view (×100).


Blade
Platform
A
B
C
D
E
F
G
H
Anterior
Posterior

species recovered. Only for the three species of *Vjalovognathus* do we make any detailed observations.

Genus ***Hindeodus*** Rexroad & Furnish, 1964

Comments. We illustrate elements of *Hindeodus* from the Callytharra, Coyric, and Noonkanbah Formations. There are potentially three species present, but the one from the Callytharra Formation lacks a preserved anterior blade margin, the one from the Coyrie Formation is a juvenile and material from the Noonkanbah Formation has a general resemblance to *Hindeodus typicalis* (Sweet) but has prominent anterior blade denticles.

Hindeodus sp. 1

Fig. 12D–I

Material studied. 7 elements (5 Pa, 2 S).

Remarks. Robust *Hindeodus* Pa element with large cusp. The anterior margin of all of the recovered elements is broken.

Stratigraphic range. Southern Carnarvon Basin, Callytharra Formation.

Hindeodus sp. 2

Fig. 12A–C

Material studied. 1 element (Pa).

Remarks. Juvenile element with cusp and 7 denticles. The anterior margin from cusp tip to antero-basal corner is concave with no indication of denticle development.

Stratigraphic range. Southern Carnarvon Basin, Coyrie Formation.

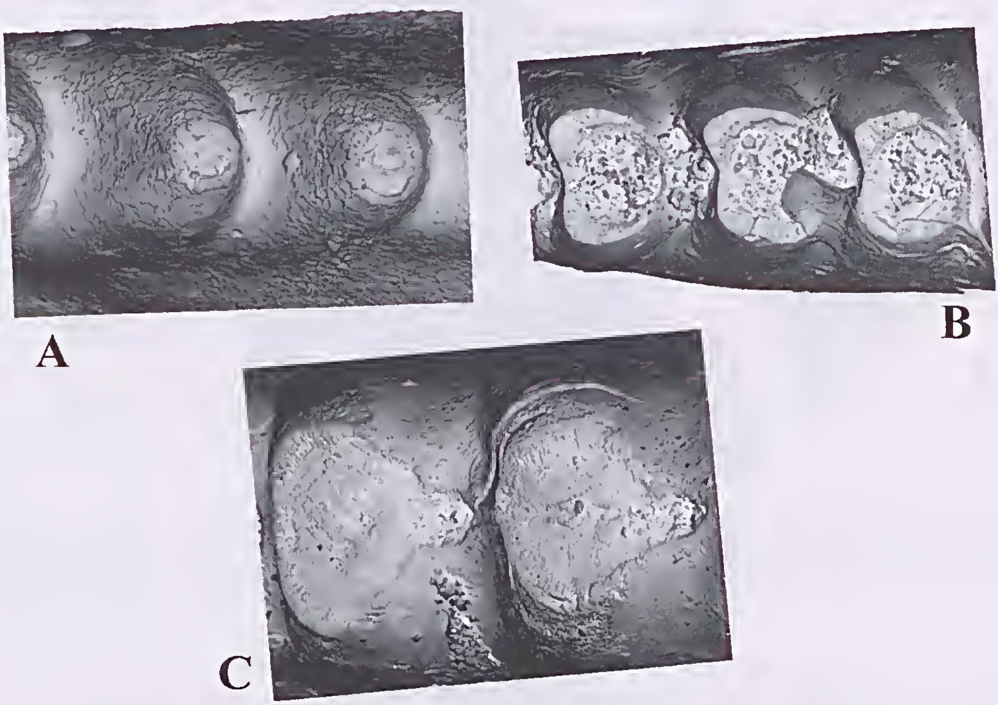


Fig. 10. Enlargement of the denticles of *Vjalovognathus* species: A, *V. australis* (×500), see Fig. 9B, denticles 4 and 5 from broken blade tip; B, *V. shindyensis* (×360), see Figs 9D and 23E, denticles 6 to 8 from blade tip; C, *V.* sp. nov. A (×470), see Fig. 9G, denticles 4 and 5 from blade tip.

Hindeodus sp. 3

Fig. 13A–G

Material studied. 21 elements (18 Pa, 1 Pb, 2 S).

Remarks. A partial apparatus of this species of *Hindeodus* is present in the material, but preservation is generally poor and most of the elements are broken. The Pa element has a projecting anterior blade with at least 3 denticles developed. The Pb element (Fig. 13B, C) is similar to a form that Igo (1981) called *Xainognathus sweeti*.

Stratigraphic range. Canning Basin, Noonkanbah Formation.

Genus **Mesogondolella** Kozur, 1988

Type species. *Gondolella bisselli* Clark & Behnken 1971.

Comments. We follow the Kozur (1989) differentiation of *Mesogondolella*.

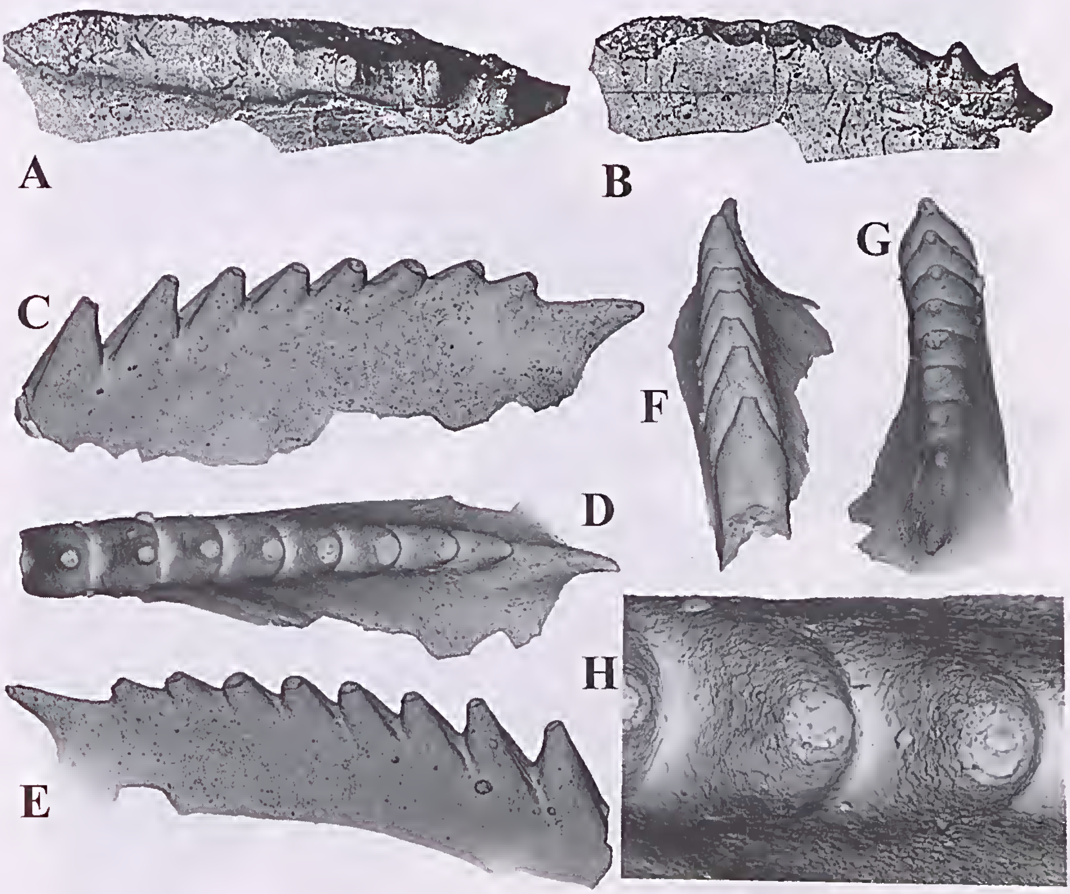


Fig. 11. A–B, *Vjalovognathus shindyensis* (Kozur) left Pa element, holotype specimen of Kozur & Mostler (1976): A, oral view; B, oblique oral-inner lateral view. C–H, *Vjalovognathus australis* sp. nov., holotype, right Pa element (CPC 34644) [Timor, Barkham SB-18], all views ×155, except as noted: C, inner lateral view; D, oral view; E, outer lateral view; F, anterior view; G, oblique oral-posterior view; H, enlargement (×500) of denticles 4 and 5 located on the anterior part of the platform, note shallow groove on the anterior margin and gently rounded posterior margin (anterior to left).

Mesogondolella idahoensis
(Youngquist, Hawley & Miller, 1951)
Figs 8A, 14–20

Material studied. 39 elements (30 Pa, 2 Pb, 3 M, 2 Sa, 1 Sc, 1 Sb).

Comments. The Pa elements represented in our faunas are closely comparable with those of *Mesogondolella idahoensis* that have been widely described and illustrated in the literature. Our material is however fragmentary and somewhat poorly preserved. We consider the apparatus to be a typical septimembrate one conforming to the standard Permian–Triassic apparatus style that has been well illustrated in the literature. We believe the over-representation of Pa elements is due to these being more robust than the other elements that were separated post-mortem by winnowing.

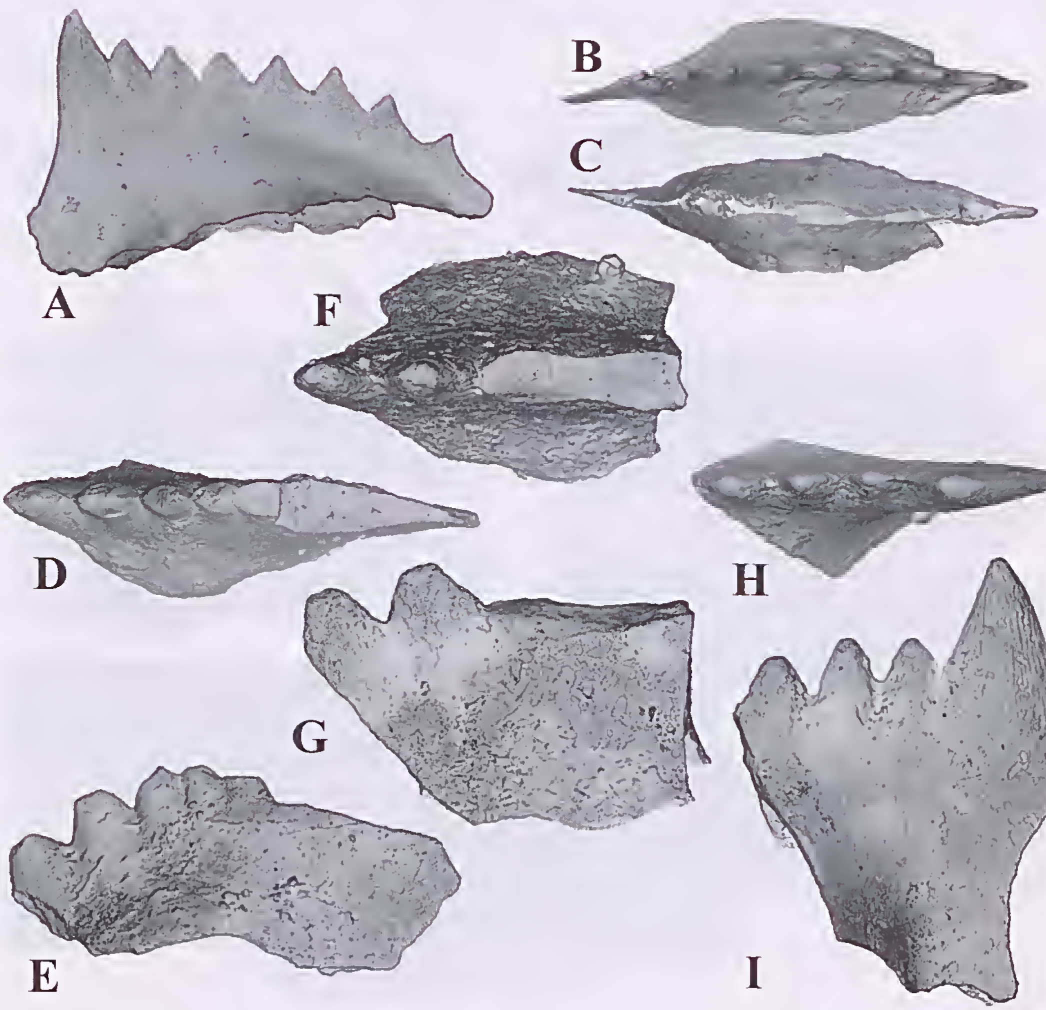


Fig. 12. Hindeodus sp. A–C, Pa element (CPC 34645) [CB 34/01], all views ×160: A, inner lateral view; B, oral view; C, aboral view. D–E, Pa element (CPC 34646) [CB 02/10], all views ×140: D, oral view; E, lateral view. F–G, Pa element (CPC 34647) [CB 02/10], all views ×150: F, oral view; G, lateral view. H–I, Pa element (CPC 34648) [CB 02/10], all views ×200: H, oral view; I, lateral view.

Age range. Early Kungurian, *Mesogondolella idahoensis–Vjalovognathus shindyensis* Zone in Australia.

Stratigraphic recovery. Canning Basin, Noonkanbah Formation.

Genus **Vjalovognathus** (Kozur, 1977)

Type species. Vjalovites shindyensis Kozur 1976.

Revised diagnosis. Multimembrate conodont apparatus of at least six element types and probably conforming to the septimembrate apparatus structure as found in gondolellids. Elements recognised include Pa, Pb, M, Sb, Sc and Sd forms. The Pa element is deeply excavated with a thin-walled crown structure. The S and M elements have relatively enlarged basal cavities, but the crown wall is thicker than that of the Pa elements. The Pa element is segminiscaphate with the cusp located at the posterior margin of a broad, deeply excavated and thin-walled basal cavity and the posteriorly inclined denticles extend forward into a narrow but

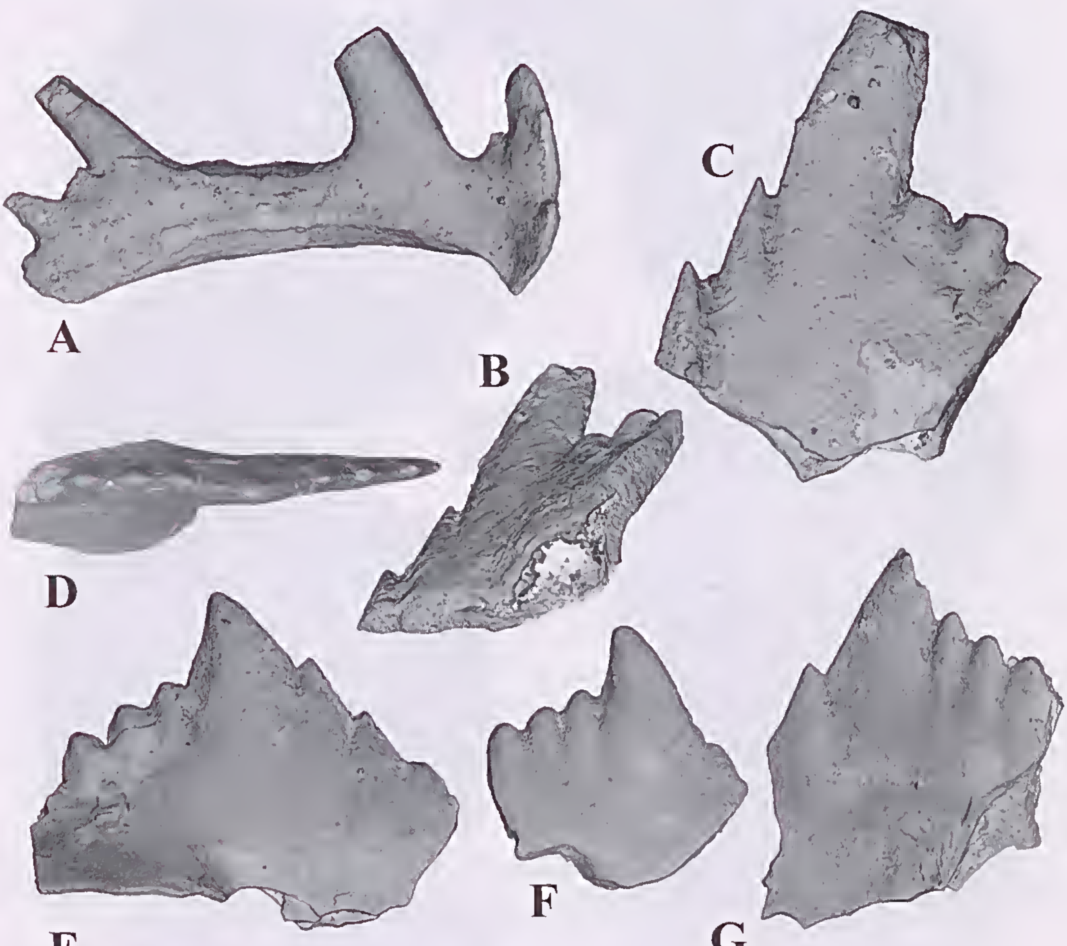


Fig. 13. Hindeodus sp. All views ×120 except as noted. A, right Sc element (CPC 34649) [WCB 902/2A] inner lateral view. B–C, left Pb element (CPC 34650) [WCB 902/2A]: B, oblique aboral-inner lateral view (×225); C, inner lateral view (×225). D–E, left Pa element (CPC 34651) [WCB 902/2A]: D, oral view; E, inner lateral view. F, left Pa element (CPC 34652) [WCB 902/2A] inner lateral view. G, right Pa element (CPC 34653) [WCB 902/2A] inner lateral view.

deeply excavated anterior blade. The Pb element is anguliscaphate with a long anterior process and a short posterior process. The M element is makellate with two denticles on the short inner lateral process. The Sb and Sc elements are bipennate with a reduced posterior process and a denticulate anterior process. The Sd element is digyrate. An Sa element has not yet been recognised.

Remarks. Most of the elements of *Vjalovognathus* recovered in this study are poorly preserved Pa elements. Their scaphate morphology, with thin walls over the enlarged basal cavity, make these elements inherently fragile and subject to breakage. A total of only 12 Pb, M and S elements have been recovered from the three species studied. The posterior processes of the Pb, Sc and Sd elements are short and adentate. The outer lateral

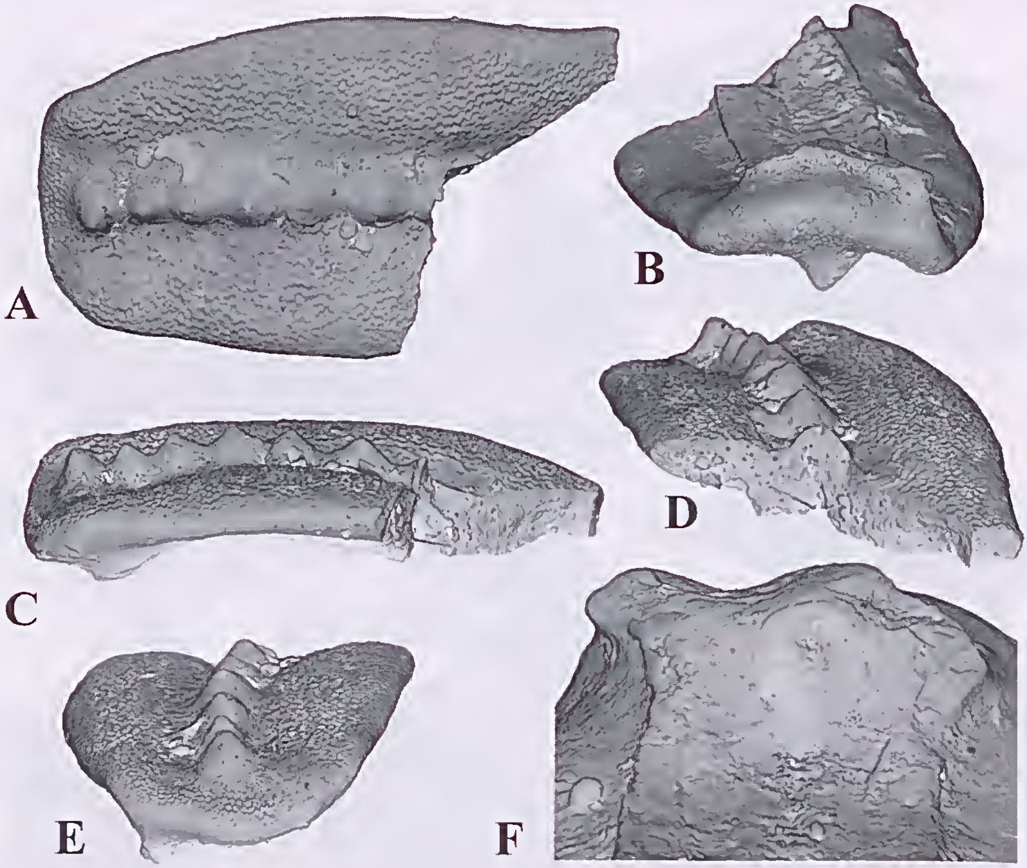
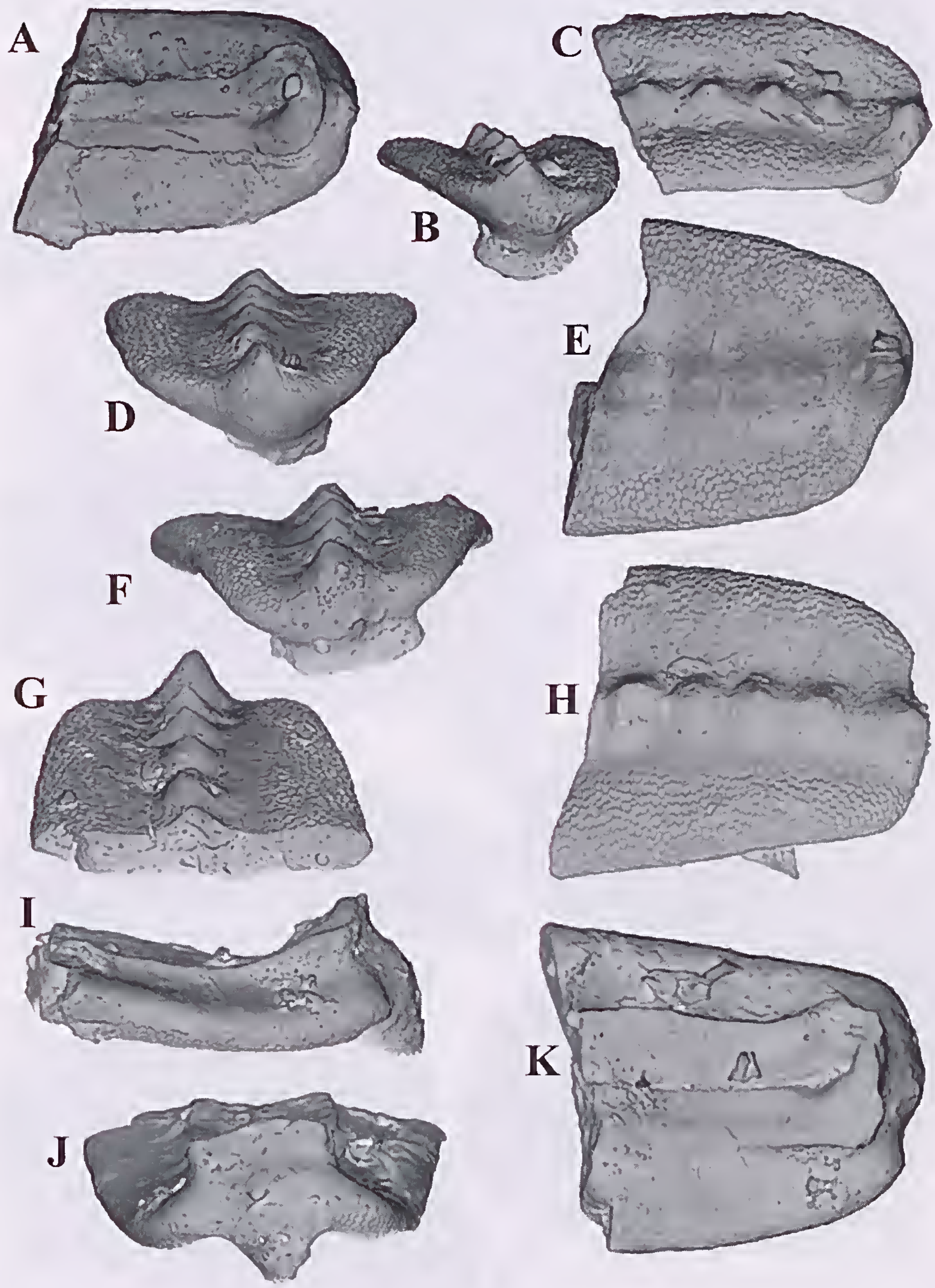


Fig. 14. Mesogondolella idahoensis, Pa element. All figures ×100 except as noted. A–F, left element (CPC 34654) [WCB 902/2A]: A, oral view; B, posterior-aboral view; C, inner lateral view; D, anterior view; E, anterior-oral view; F, enlargement (×220) showing pits at posterior end of the aboral surface.

Fig. 15. Mesogondolella idahoensis, Pa elements. All views ×150. A–C, right element (CPC 34655) [WCB 902/2A]: A, aboral view; B, posterior-oral view; C, oral view. D–E, left element (CPC 34656) [WCB 902/2A]: D, posterior-oral view; E, oral view. F–K, right element (CPC 34657) [WCB 902/2A]: F, posterior-oral view; G, anterior-oral view; H, oral view; I, outer-lateral view; J, posterior-aboral view; K, aboral view.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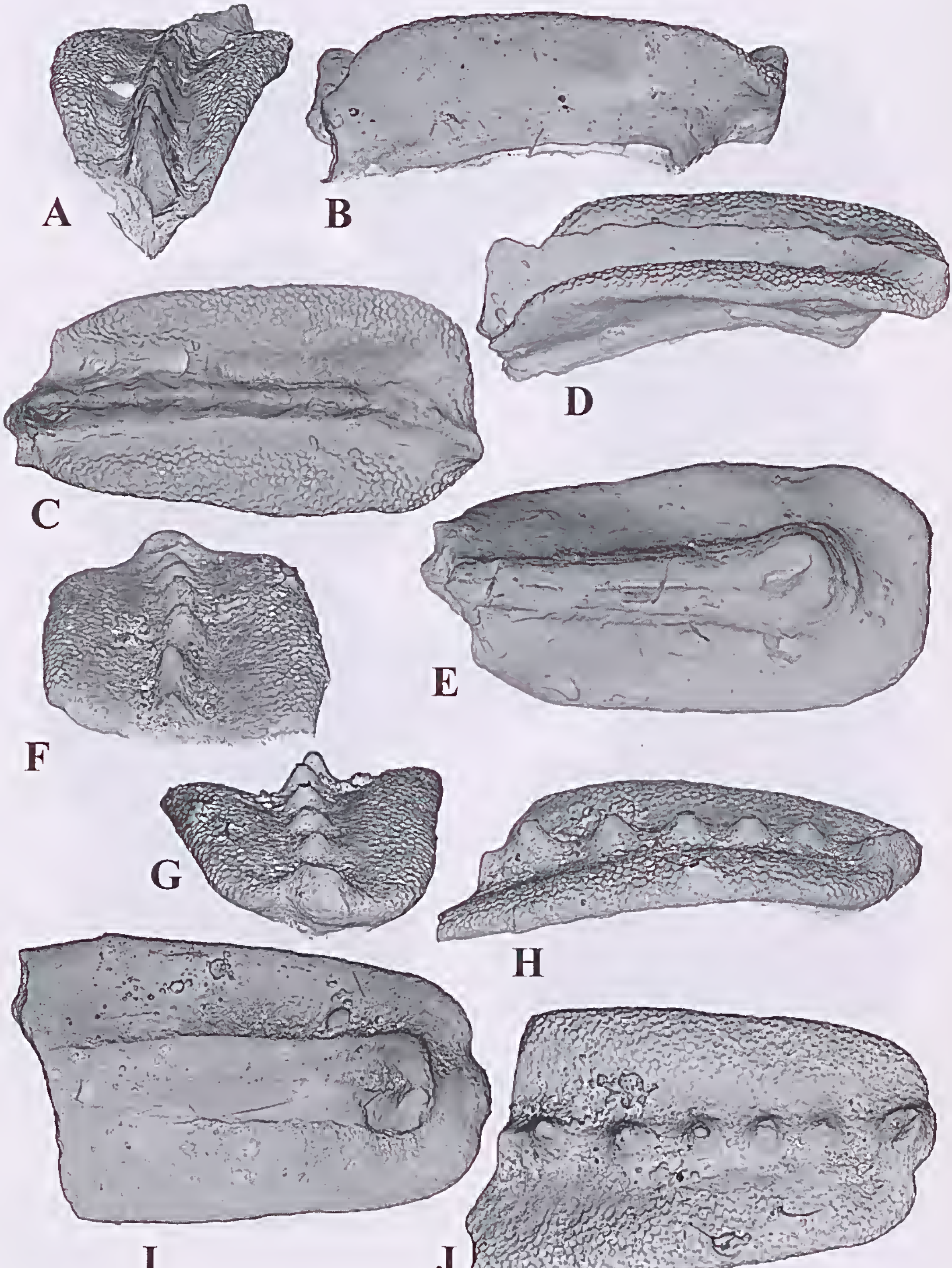
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process of the single M element recovered is broken. No Sa element has been recovered in our collections, but one would be expected because the rest of the elements of this apparatus conform to the 'normal' septimembrate apparatus structure of Upper Palaeozoic conodonts such as *Mesogondolella*, *Diplognathus* or *Neostreptognathodus*.

Kozur (in Kozur & Mostler 1976) provided only a brief diagnosis and description of the Pa element of a monoelemental *Vjalovognathus shindyensis* and his illustrations (Kozur & Mostler 1976: pl. 3, figs 9, 11) are not adequate to make anything other than a few general observations about the genus or species. Subsequent illustration of *V. shindyensis*

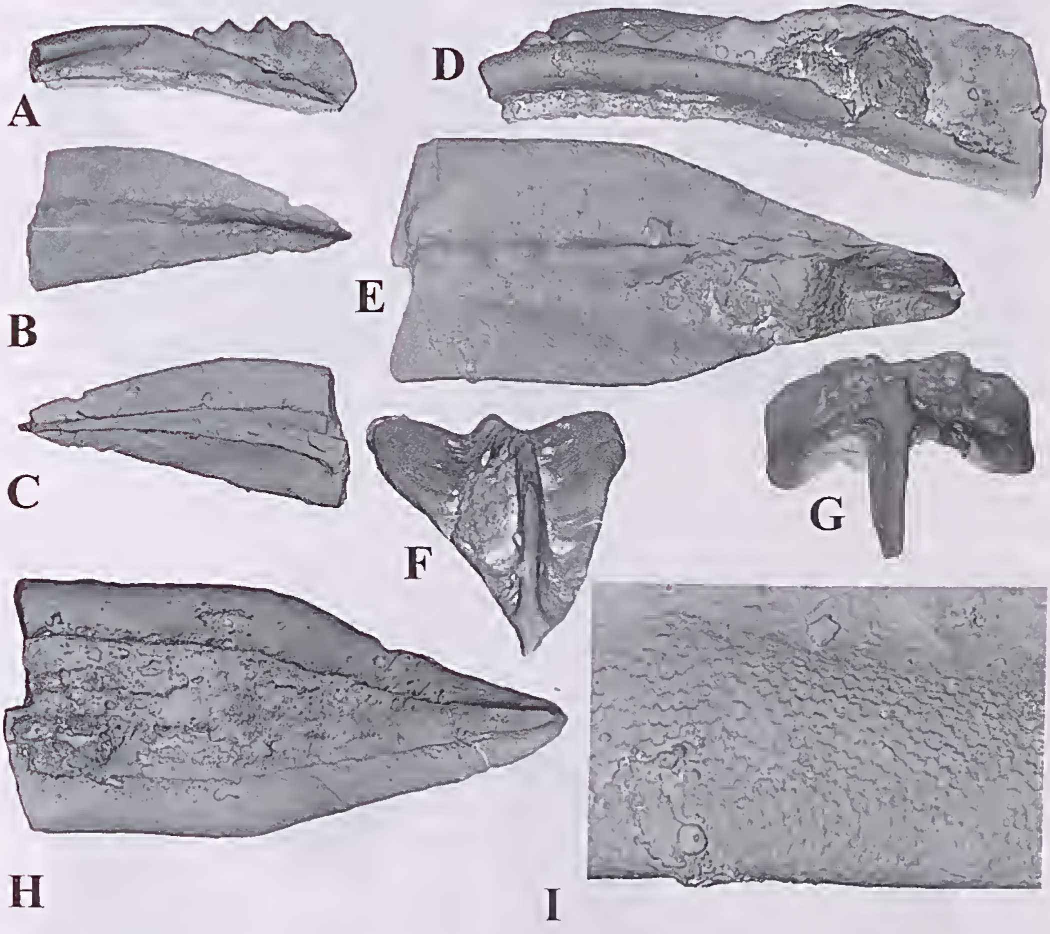
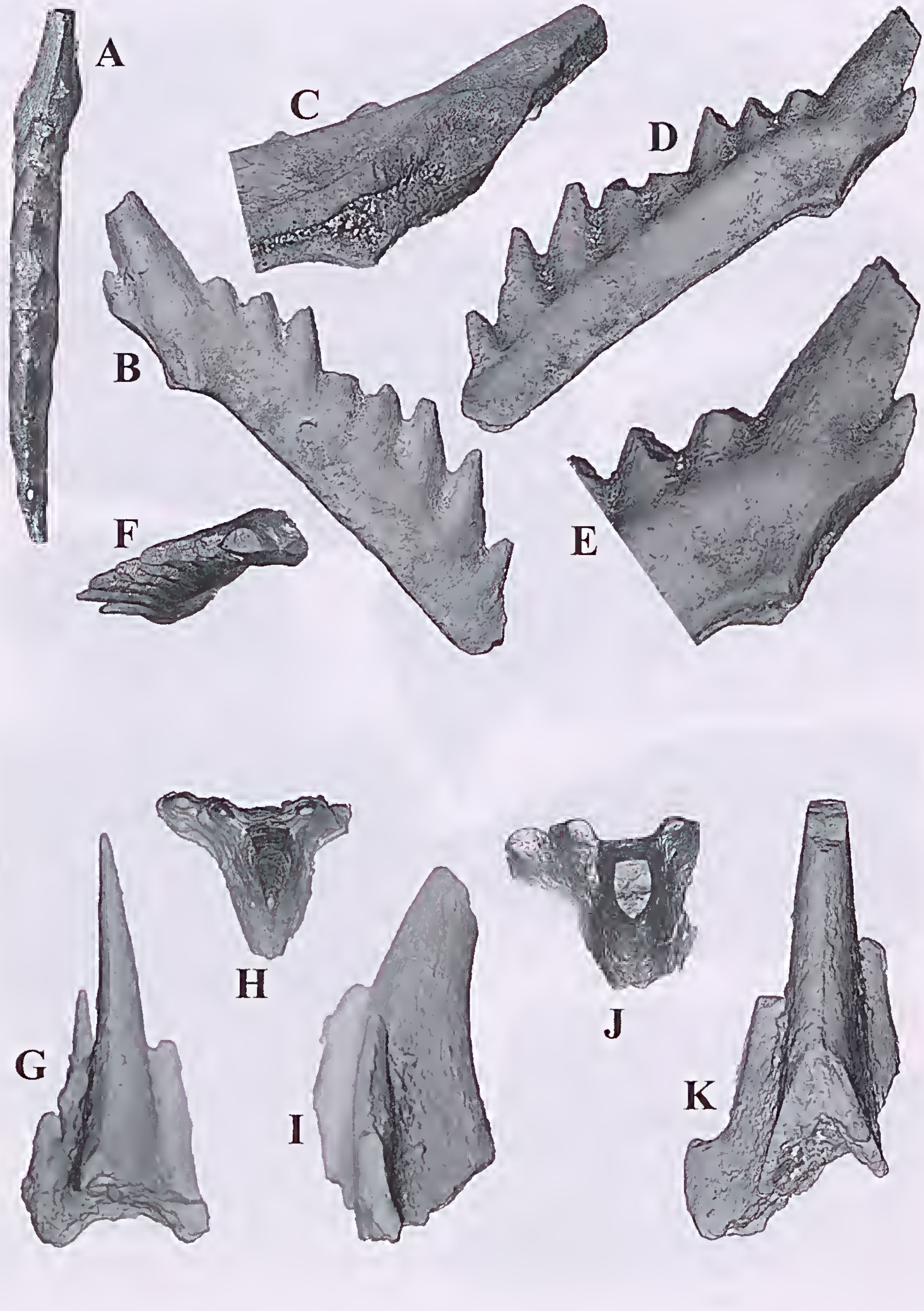


Fig. 17. Mesogondolella idahoensis, Pa elements. All views ×70, except as noted. A–C, left element (CPC 34660) [WCB 902/2A]: A, inner lateral view; B, oral view; C, aboral view. D–I, left element (CPC 34661) [WCB 902/2A]: D, inner lateral view; E, oral view; F, anterior view; G, anterior-basal view; H, basal view; I, enlargement (×200) showing reticulate pattern on oral surface of the platform margin.

Fig. 16. Mesogondolella idahoensis, Pa elements. All views ×165. A–E, right element (CPC 34658) [WCB 902/2A]: A, anterior-oral view; B, inner lateral-basal view; C, oral view; D, inner lateral-oral view; E, basal view. F–J, left element (CPC 34659) [WCB 902/2A]: F, anterior-oral view; G, posterior-oral view; H, outer lateral oral view; I, aboral view; J, oral view.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(Kozur 1978: pl. V, figs 1, 9) provides enough definition of the cross-section of the denticle morphology of the Pa element to allow confirmation of species discrimination within the genus. Kozur (1996, pers. comm.) provided a photocopy of unpublished photographs of the type specimen that we use here to better illustrate the morphology of the type specimen of the genus (Fig. 11A, B). Kozur (1978) has made several references to an earlier species of *Vjalovognathus*, his *V.* sp. nov., but this form has not been illustrated and its possible relationship to our species determinations is unknown.

The morphology of the Pa element of *Vjalovognathus* (Fig. 9) is essentially similar to that of the Pa elements of *Gondolella* or *Neogondolella* (Kozur, 1989). The element is oriented with the narrow blade anterior and the cusp posterior. The oral surface of the element has a carina with denticles extending from the anterior margin to the posterior cusp. The element has a scaphate morphology with a large open basal cavity. The platform-blade separation is made at the point where the basal margin begins to flare outward.

In this study we have been able to differentiate three species of *Vjalovognathus*, based principally on the cross-sectional shape of the denticles (Fig. 10) and cusp (Fig. 9) of the Pa elements. Denticles of *V. australis* are essentially round with a narrow groove on the anterior margin of some denticles. Denticles of *V. shindyensis* are laterally expanded and have a broader groove on the anterior margin that gives larger denticles a kidney-bean shape in section view near the denticle base; denticles on the platform tend to be tightly nested. Elements of *V.* sp. nov. A have an ovate to diamond shaped cross-section that is associated with the development of an axial ridge keel on both anterior and posterior margins of the denticles. Wardlaw (1997, pers. comm.) has provided illustrations of the Pa elements of what is certainly a fourth species of *Vjalovognathus* from the upper part of the Chhidru Formation in the Salt Range of Pakistan. In juvenile specimens of the Chhidru material the axial ridge links adjacent denticles and in adult specimens the softer core material is removed to form a trough along the oral margin. The single specimen from the Selong section is much obscured by mineral overgrowth and cannot be specifically identified.

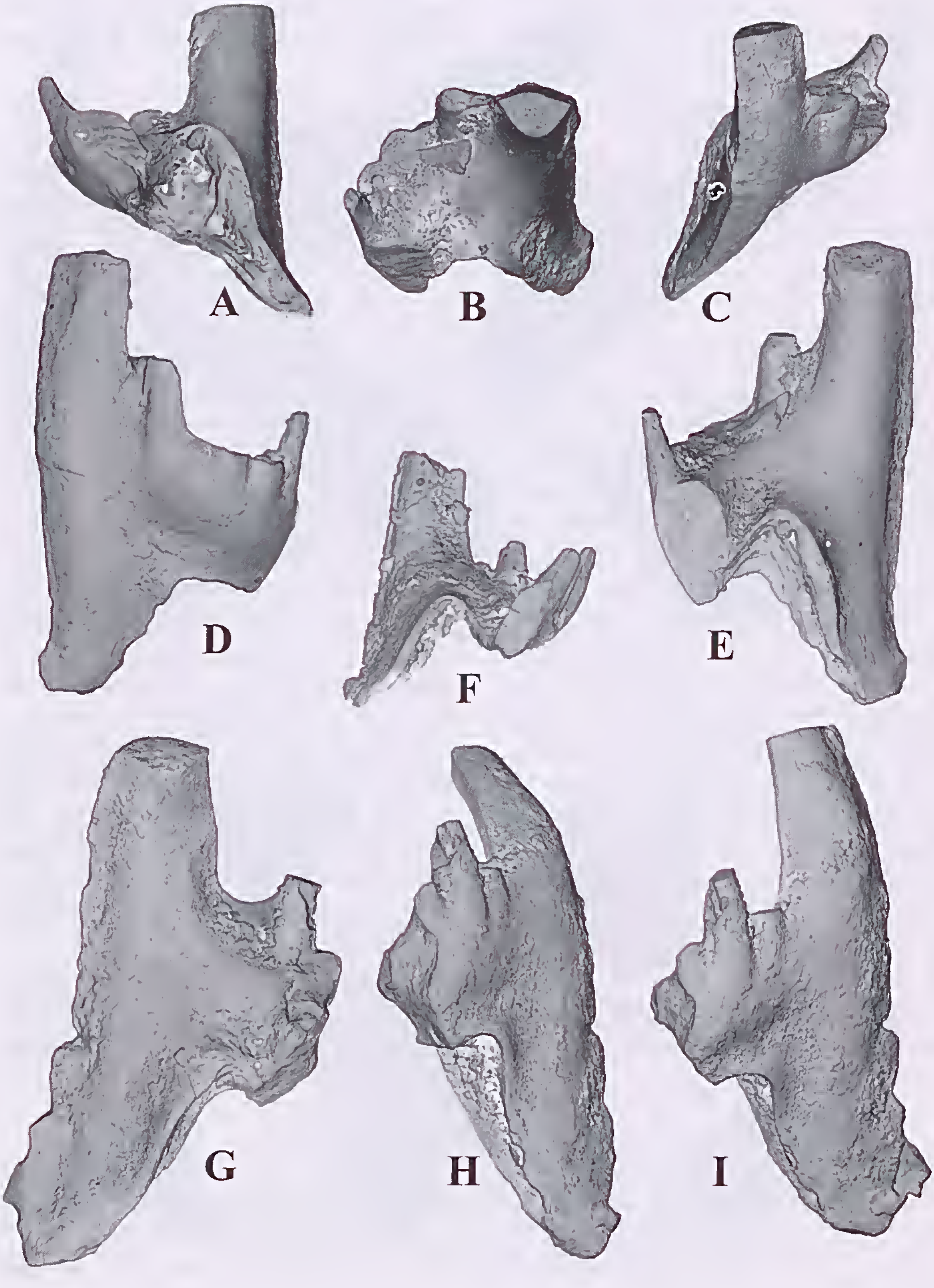
Truncation of oral surface denticles

Vjalovognathus Pa element denticulation is typically truncated a short distance above the oral surface (Fig. 9). Denticles of the S, M and Pb elements do not develop a similar pattern of denticle truncation with all elements having pointed denticle tips. In the Pa element only the anterior one or two denticles of the blade and the posteriorly located cusp retain a normal denticle morphology. This denticle truncation appears to be primary, that is to have taken place when the element was part of the living animal. It has been observed on all of the *Vjalovognathus* Pa elements recovered from any location (Kozur & Mostler 1976; van den Boogaard 1987; Reimers 1991; Wardlaw 1997, pers. comm.). The concentrically laminated tissue in the central part of the truncated denticle appears to be slightly softer than the outer tissue layer. Many elements thus show a slight depression in the central part of the denticle (Fig. 21F). Where adjacent denticle cores are linked, as in the case of material from the Chhidru Formation of Pakistan (Bruce Wardlaw 1997, pers. comm.) the result may be a trough extending along the oral margin.

However, the cause of this denticle tip truncation remains elusive. While no paired Pa elements have been recovered from bedding plane assemblages or fused clusters, if element left and right lateral photographs are reversed and placed in opposition, the slope of the truncated denticle surface (Figs 9, 21J) is down toward the posterior, such that it does not appear to be possible that opposed element cusp tips could have caused the truncation by abrasive wear.

Kozur (1989: 423) recognised three types of carina development in gondollelid Pa elements. Carina type *a* has high anterior (blade) denticles, low or fused denticles in mid-length and higher

Fig. 18. Mesogondolella idahoensis, Pb and Sa elements. A–F, right Pb element (CPC 34662) [WCB 902/2A], all views ×105, except as noted: A, oral view of anterior process; B, outer lateral view; C, oblique view (×185) of broken posterior process and basal cavity; D, inner lateral view; E, enlargement (×185) showing striae on cusp; F, oral view of cusp showing cross-section shape. G–H, Sa element (CPC 34663) [WCB 902/2A], all views ×220: G, posterior view; H, oral view. I–K, Sa element (CPC 34664) [WCB 902/2A], all views ×230: I, left lateral view; J, oral view; K, posterior view.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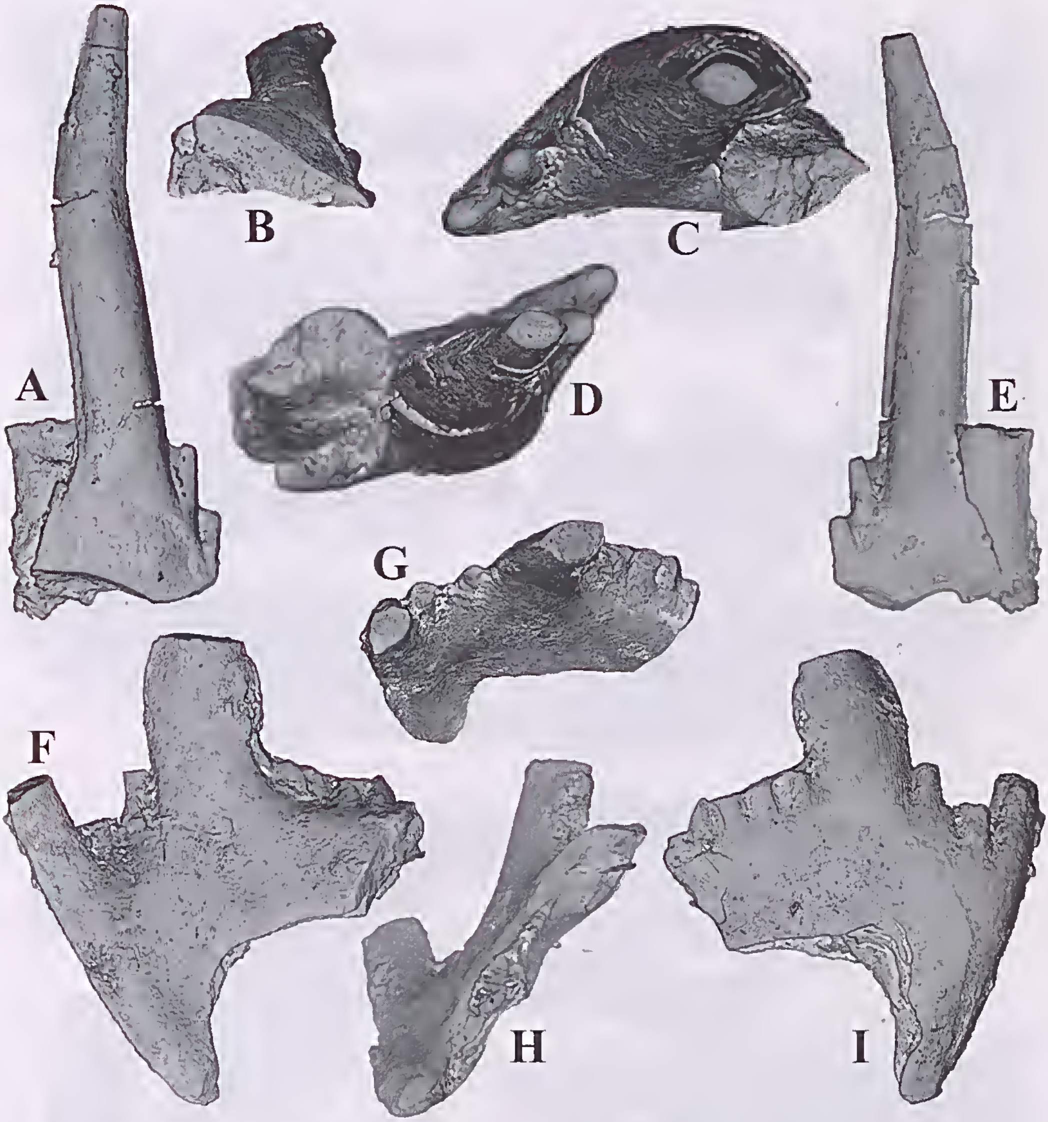

Fig. 20. *Mesogondolella idahoensis*, Sc and Sd elements. A–E, Sd element (CPC 34668) [WCB 902/2A] broken and fractured element, all views ×245 except as noted: A, inner lateral view; B, aboral view; C, oral view (×500); D, oblique oral view (×500); E, outer lateral view. F–I, Sc element (CPC 34669) [WCB 902/2A], all views ×200: F, inner lateral view; G, oral view; H, aboral view; I, outer lateral view.

Fig. 19. *Mesogondolella idahoensis*, M elements. All views ×225. A–E, right M element (CPC 34665) [WCB 902/2A]: A, oblique aboral-posterior view; B, oral view; C, oblique anterior-inner lateral view; D, anterior view; E, posterior view. F, right element (CPC 34666) [WCB 902/2A] oblique aboral-inner lateral view (×200). G–I, right element (CPC 34667) [WCB 902/2A]: G, inner lateral view; H, oblique outer-lateral view; I, outer lateral view.

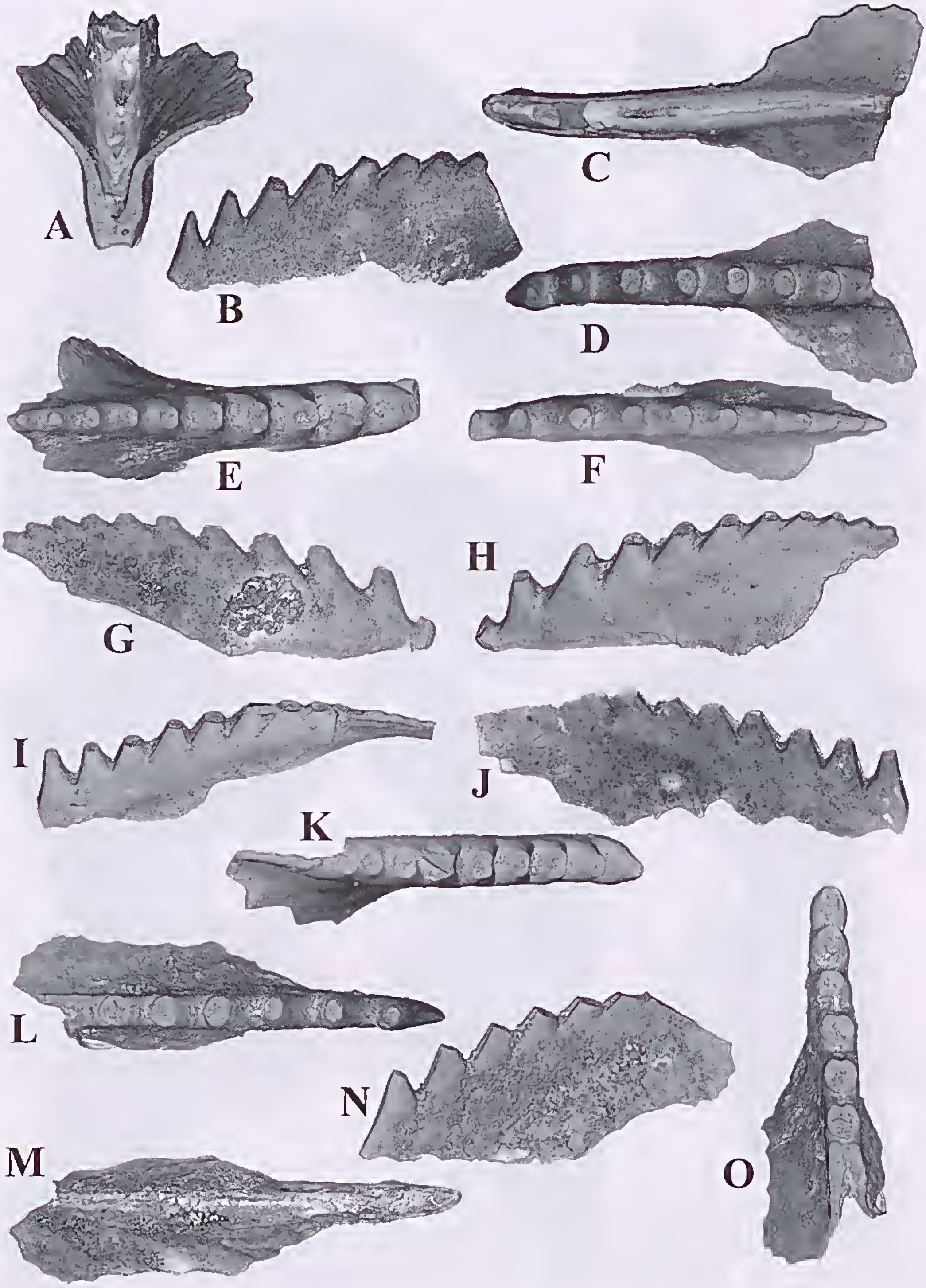

Fig. 21 (see legend on page 447)

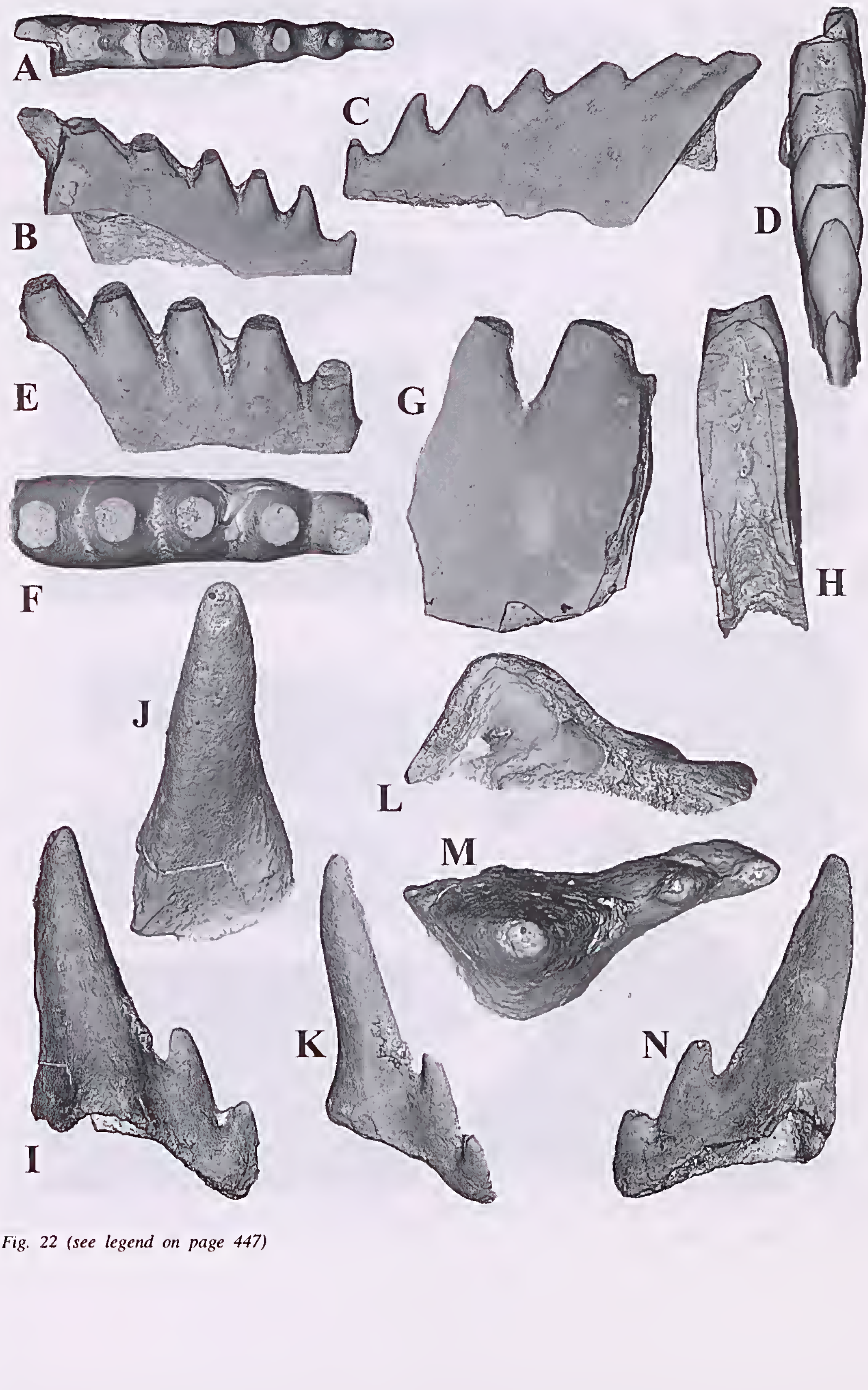

Fig. 22 (see legend on page 447)

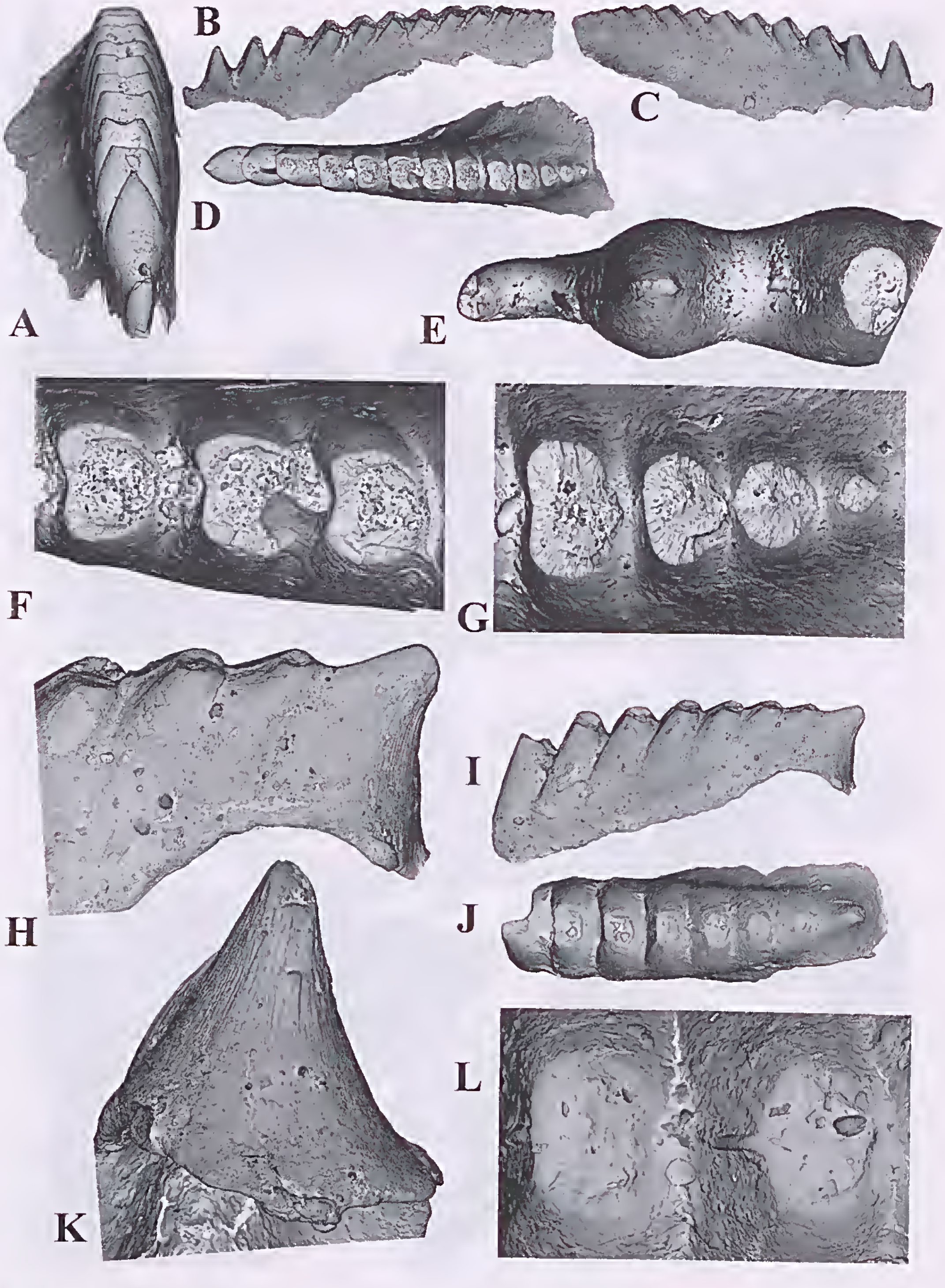

Fig. 23 (see legend on page 447)

denticles near the posterior end. This style of carina is most commonly developed in *Mesogondolella* and *Neogondolella* (Kozur 1989), and is very similar to the pattern observed in *Vjalovognathus*.

Origin and evolutionary trends in Vjalovognathus

Kozur (in Kozur & Mostler 1976) has suggested that *Vjalovognathus* has evolved from *Neostreptognathodus*, probably *N. pequopensis* or a similar form. This study suggests that Kozur's interpretation cannot be substantiated by subsequent work. Firstly, *V. australis*, as demonstrated by van den Boogaard (1987) and Reimers (1991), first appears with *Mesogondolella bisselli* prior to the first appearance of *N. pequopensis*. Secondly, the morphology of the apparatus elements of *Vjalovognathus* are unlike those associated with species of *Neostreptognathodus* (Sweet 1988).

This study demonstrates that *Vjalovognathus* has evolved from the lineage of naked gondolellids (von Bitter & Merrill 1980) by the development of a segminiscaphate basal surface in the Pa element crown. The anguliscaphate morphology of the *Vjalovognathus* Pb element is also very similar to that of the Pb element of the naked gondolellids. *Gondolella postdenuda* von Bitter & Merrill (von Bitter & Merrill 1980), of Late Pennsylvanian (Virgilian) age, is a possible direct ancestor of *Vjalovognathus*. The ramiform elements of *Gondolella sublanceolata* Gunnell, *G. postdenuda*, *Mesogondolella idahoensis* and *V. shindyensis* have similar morphologies, the bipennate Sc and Sb elements of all species being characterised by short posterior and long anterior processes (von Bitter 1976). These species also have digyrate Sd elements. This concept is supported by the general morphology of the Pa elements of *Gondolella*, *Vjalovognathus* and *Mesogondolella* which have a denticulate anterior blade and a low cusp that is posteriorly located and directed. The associated Pb elements (Fig. 8) have a long anterior process and a very short posterior process.

We cannot identify an immediate predecessor for *V. australis*, the oldest recorded species of the genus. We anticipate that there should be a species with a less expanded basal cavity in sediments older than the upper Sakmarian occurrence of *V. australis*.

Legends to Figs 21–23.

Fig. 21. Vjalovognathus australis, Pa elements. All views ×65. A–D, right element (CPC 34670) [CB 02/10]: A, posterior-basal view; B, inner lateral view; C, aboral view; D, oral view showing 5 blade denticles. E–H, right element (CPC 34671) [CB 04/15]: E, oblique oral-posterior view; F, oral view; G, outer-lateral view; H, inner lateral view. I–K, right element (CPC 34672) [CB04/97]: I, inner lateral view; J, outer lateral view; K, oral view. L–O, left element (CPC 34673) [CB 04/15]: L, oral view; M, aboral view; N, inner lateral view; O, oblique oral-anterior view.

Fig. 22. Vjalovognathus australis, Pa and Pb elements. All views ×130, except as noted. A–D, Pa element fragment (CPC 34674) [CB 22/01]: A, oral view (×70); B, lateral view (×70); C, reverse lateral view (×70); D, anterior view (×70), note that anterior-most two denticles have pointed tips and the rest of the denticles are progressively truncated closer to the blade surface. E–F, Pa element fragment (CPC 34675) [CB 02/10]: E, lateral view; F, oral view. G–H, Pa element fragment (CPC 34676) [CB 05/10]: G, lateral view (×145); H, end view showing preserved attachment cone (×145). I–N, right Pb element (CPC 34677) [CB 01/12]: I, outer lateral view; J, oblique posterior view; K, outer-anterior view; L, aboral view; M, oral view; N, inner lateral view.

Fig. 23. Vjalovognathus shindyensis, Pa elements. A–G, left element (CPC 34678) [CB 36/02]: A, anterior view (×110); B, outer lateral view (×70); C, inner lateral view (×70); D, oral view (×70); E, enlargement (×360) of anterior tip of blade showing new denticle, second denticle with pointed tip and third denticle with flattened top; F, enlargement (×360) of blade denticles 6 to 8 showing appressed denticles; G, enlargement (×360) showing platform denticles 11 to 14 that decrease in size toward cusp. H–L, left element (CPC 34679) [Frome Rocks 1, 1099–1109 ft]: H, enlargement (×300) of lateral view of cusp and posterior three platform denticles; I, enlargement (×475) of posterior margin of cusp showing striae; J, outer lateral view (×125); K, oral view (×125); L, enlargement (×600) showing keel on anterior edge of denticles.

Vjalovognathus shindyensis (Kozur)

Figs 9, 11, 21–26

Vjalovites shindyensis Kozur 1976—Kozur & Mostler 1976: 20, pl. 3, figs 9, 11.
Vjalovognathus shindyensis (Kozur)—Kozur 1977: 121—Kozur 1978: 106, pl. 5, figs 1, 9.

Material studied. 168 elements (159 Pa, 1 Pb, 1 M, 4 Sc, 1 Sb, 2 Sd).

Diagnosis. Multimembrate apparatus, probably septimembrate, with six element types defined. Pa element segminiscaphate with cusp located posteriorly, denticle cross-section ovate to kidney-bean shaped and linearly compressed at base with an anterior groove, and basal cavity deeply excavated. Pb element anguliscaphate with long anterior process and short or adentate posterior process. M element is makellate with denticulate inner and outer lateral processes. Sb and Sc

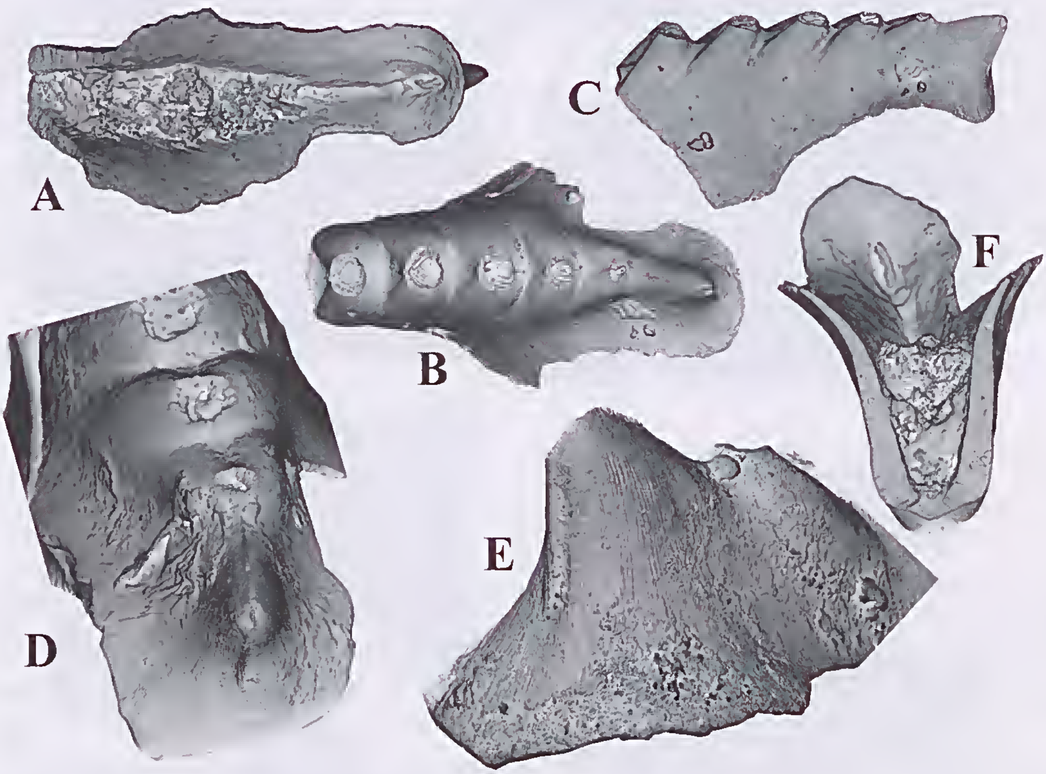

Fig. 24. Vjalovognathus shindyensis, Pa element. All views ×135 except as noted. A–F, right element (CPC 34680) [CB 41/01]: A, aboral view; B, oral view, note broken basal margin; C, inner lateral view; D, enlargement (×245) of cusp and posterior platform denticles; E, enlargement (×445) of outer lateral view of nearly smooth cusp; F, anterior view into basal cavity showing sub-parallel sides of blade prior to outward flare of the platform.

Fig. 25. Vjalovognathus shindyensis, Pb and Pa elements. A–C, Pa element (CPC 34681) [CB 41/01], all views ×125: A, oral view; B, outer lateral view showing two pointed tip denticles at anterior end of blade; C, anterior view. D–F, right Pa element (CPC 34682) [Frome Rocks 1, 1099–1109 ft], all views ×110: D, inner lateral view, note broken basal margin; E, oral view; F, outer lateral view. G–I, left Pa element (CPC 34683) [Frome Rocks 1, 1099–1109 ft], all views ×145: G, oral view; H, inner lateral view; I, outer lateral view. J–N, right Pb element (CPC 34684) [WCB 902/2A], all views ×150: J, inner lateral view; K, outer lateral view; L, oblique oral-anterior view; M, oral view; N, aboral view.


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elements are bipennate with denticulate anterior process and reduced or adentate posterior process. The Sd element is fragmentary but appears to be digyrate with broken processes. All elements with smooth crown surface texture, lacking striae except around the cusp on some of the Pa elements, but with a low axial ridge that may be weakly developed along the axial plane of cusp and

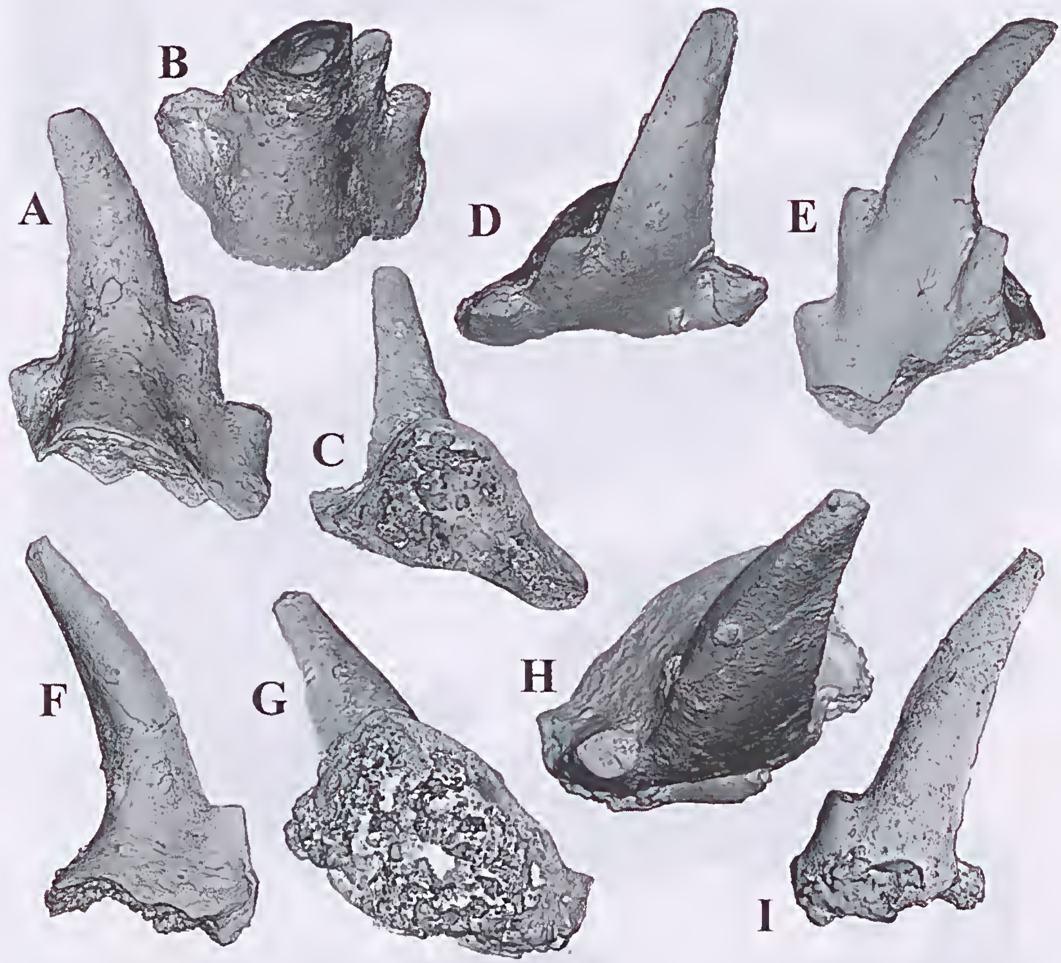
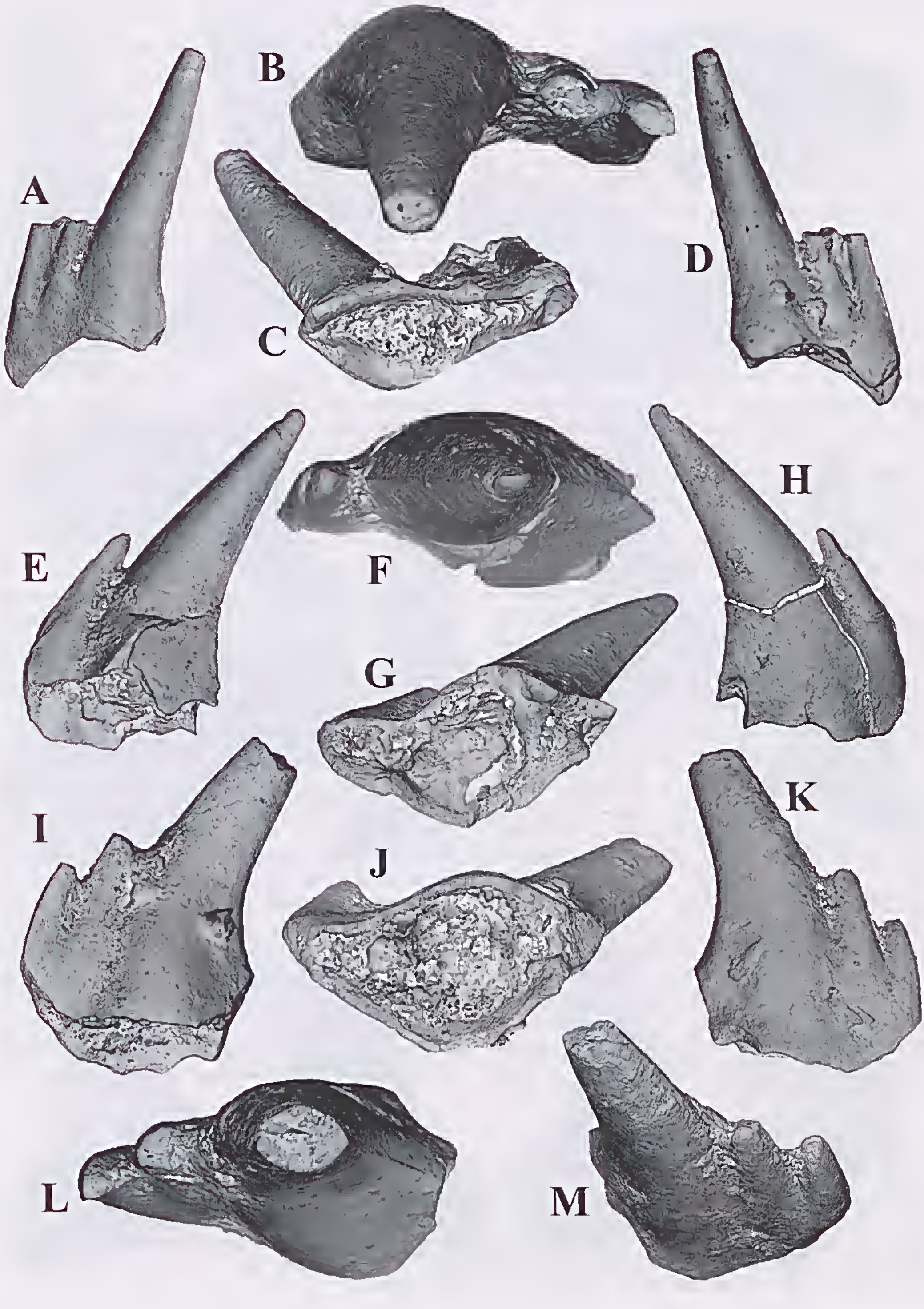


Fig. 26. Vjalovognathus shindyensis, M elements. All views ×165, except as noted. A–E, left element (CPC 34685) [WCB 902/2A]: A, posterior view; B, oral view on cusp tip; C, aboral view; D, oral view on base of element; E, anterior view. F–I, left element (CPC 34686) [WCB 902/2A]: F, posterior view; G, enlargement (×245) of aboral view; H, enlargement (×245) of oral view; I, anterior view.

Fig. 27. Vjalovognathus shindyensis, Sc elements. A–D, left element (CPC 34687) [WCB 902/2A]: A, outer lateral view (×160); B, oral view (×340); C, aboral view (×270); D, inner lateral view (×160). E–H, right element (CPC 34688) [WCB 902/2A]: E, inner lateral view (×170); F, oral view (×315); G, aboral view (×260); H, outer lateral view (×172). I–M, right element (CPC 34689) [WCB 902/2A]: I, inner lateral view (×225); J, aboral view (×300); K, outer lateral view (×225); L, oral view (×375); M, oblique oral-outer lateral view (×225).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denticles. Cross-section plan of cusp and denticles of Pb, M and S elements laterally compressed and biconvex in axial plane.

Description. All of the differentiated elements of *Vjalovognathus shindyensis* (Kozur) are deeply excavated, scaphate forms with thin-walled flanges to denticulated processes. The external surface of all elements is smooth, lacking striae except around the cusp on a couple of the Pa elements, but with a weak ridge developed along the axial plane of the cusp and denticles of some elements. Cusp and denticles of the Pb, S and M elements are laterally compressed and biconvex on plan view. The upper part of the denticles and cusps taper to a pointed to slightly rounded tip where preserved.

The Pa element is segminiscaphate with a single row of 7 to 14 denticles and one cusp extending from the anterior blade to a posterior platform. In plan view the element is bowed slightly outward and the cusp and posterior-most denticles are twisted slightly inward. The element is differentiated into blade and platform at the point where the basal margin of the element flares abruptly outward (Fig. 9). The blade supports 3–7 denticles (Fig. 21B, D), and the platform also has from 3–7 denticles (Figs 21D, 22B). The element is deeply excavated under both the platform and blade. The oral view shows that the denticulate ridge does not become appreciably wider on the platform, but that the basal margin flares outward giving the appearance of a platform. Internally the oral cavity crest of the excavation narrows toward the posterior end. On the posterior margin, the element is broadly rounded at the basal margin, but the denticle row on the oral margin tapers abruptly over the posterior-most 3 or 4 denticles to the cusp (Fig. 21G, K). The cusp is short and stubby, projecting posteriorly upward at an angle of about 45° from the plane of the eroded oral surfaces of the denticle row and may extend slightly above the level of the denticles. The oral surface of the element is smooth except for some striae developed on the lateral and posterior margins of the cusp on two of the elements. The denticle pattern of the element changes from the anterior to the posterior ends of the element. The anterior denticles are ovate with only a small anterior groove on the denticle (Fig. 21E). Progressively the denticles become more closely spaced and the groove becomes larger. By the fourth or fifth denticle, the base of the subsequent denticle is appressed and the rounded posterior margin of one denticle is inserted into the anterior groove of the adjacent denticle (Fig. 21F). In cross-section these denticles are kidney-bean-shaped. On the platform the posterior-most denticles become rounded, shorter and smaller in diameter (Fig. 21G). In cross-section the blade is narrow at the basal margin and expands laterally and then narrows to a pointed tip (Fig. 23C). The tips of all denticles become progressively eroded toward the posterior. Some elements have a slight anterior keel on some of the denticles.

The Pb element is anguliscaphate with a relatively long anterior process that is bent inward and supports three or more denticles. The posterior process is broken or poorly preserved and no denticles are apparent. The denticle cross-sectional shape is biconvex and symmetrical. However, the cusp is asymmetrically biconvex in section view (Fig. 23M) with a relatively flattened inner face and a strongly bowed outer face. This same morphology is also reflected in the basal outline of the element with a broad outwardly protruding flange on the outer lateral margin below the cusp. The element is deeply excavated under the anterior process and in cross-section looks similar to, but more laterally compressed than the anterior blade of the Pa element.

The Sc and Sb elements, thus far differentiated, appear similar with a basic bipennate morphology. However, unlike the Pb element, both elements are strongly biconvex in the cusp cross-section. The Sc element that is best preserved has two denticles on the broken anterior process. The cusp is robust and slightly recurved posteriorly, its cross-section is equally biconvex on inner and outer sides (Fig. 25L) and the tip is pointed. It is impossible to be sure that the posterior process was adentate, but the better preserved Sc element of *V.* sp. nov. A lacks denticles on the posterior process. The elements are deeply excavated under the cusp and the excavation extends under the

Fig. 28. *Vjalovognathus shindyensis*, Sb and Sd elements. A–D, left Sb element (CPC 34690) [WCB 902/2A]: A, posterior view (×200); B, inner lateral view (×200); C, oral view (×300), compare cusp cross-section with that of the Sc element (Fig. 27L); D, aboral view (×270). E–I, left Sd element (CPC 34691) [WCB 901/02]: E, oral view of base (×180); F, oral view of cusp tip (×230); G, posterior view (×110); H, aboral view (×160); I, outer lateral view (×110). J–M, left Sd element (CPC 34692) [WCB 902/2A], all views ×140: J, outer lateral view; K, aboral view; L, anterior view; M, oblique oral-anterior view.


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processes. The Sb element is similar to the Sc element except for the cross-section of the cusp which is larger on the inner lateral side (Fig. 26C).

The two Sd elements are poorly preserved; both processes are broken at the edge of the cusp and the upper part of the cusp is broken. The element appears digyrate with a short, outwardly twisted posterior process and what is presumed to be a longer, inwardly twisted anterior process. The cusp is biconvex and pointed. The basal margin of the Sd element flares laterally on both sides.

The M element is makellate with two denticles on a short inwardly and downwardly directed inner lateral process. The outer lateral process is broken just at the edge of the cusp, but the short fragment that remains appears to be directed slightly forward and supports one denticle. The buttress on the posterior edge of the cusp is large and the cusp is bent posteriorly over the buttress.

Remarks. The type specimen of *V. shindyensis* (Kozur & Mostler, 1976) that is re-illustrated here shows the kidney-bean-shaped cross-section of the denticles on the platform (Fig. 11A, B). Differentiation of *Vjalovognathus shindyensis* from *V. australis* is best made on the oral surface morphology of the Pa elements. The denticles of *V. shindyensis* tend to be closely spaced or nested and have a kidney-bean-shaped cross-section. The denticles of *V. australis* are discrete and have a rounded to oval cross-section. The Pa elements of *V.* sp. nov. A have a diamond-shaped cross-section. The Pb elements of *V. shindyensis* and *V. australis* appear very similar. The S and M elements of *V. australis* are unknown, but the Sc element of *V.* sp. nov. A is very similar to the Sc elements of *V. shindyensis*.

Age range. Early Kungurian, *Mesogondolella idahoensis–Vjalovognathus shindyensis* Zone.

Stratigraphic recovery. Southern Carnarvon Basin, Coyrie Formation; Canning Basin, Noonkanbah Formation.

Vjalovognathus australis sp. nov.

Figs 9A–C, 11C–H, 27, 28

Vjalovognathus shindyensis (Kozur) van den Boogaard 1987: 29–31, figs 8A–F, 9B, 12F—Reimers 1991: pl. 1, figs 9, 12, 14.

Material studied. 50 elements (49 Pa, 1 Pb).

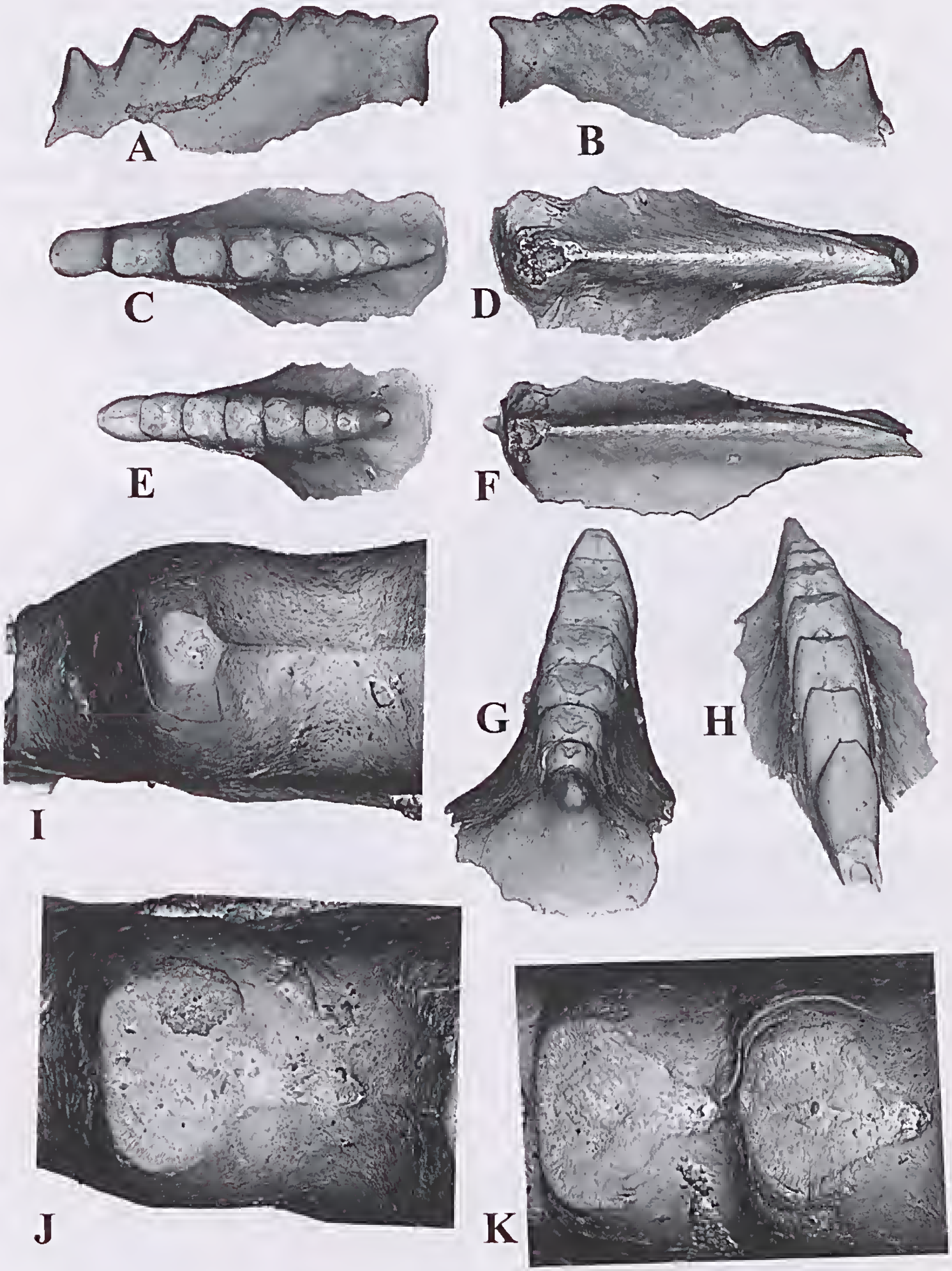
Derivation of name. From Latin 'australis' meaning southern, reflecting its southern palaeolatitude distribution.

Holotype. Pa element CPC 34644. Paratypes: Pa elements CPC 34670–6; Pb element CPC 34677 (all figured).

Diagnosis. Multimembrate apparatus, probably septimembrate, with 2 element types defined. The Pa element is segminiscaphate with cusp located posteriorly, denticles round to ovate, discrete, with a shallow anterior groove, and the basal cavity is deeply excavated. Pb element anguliscaphate with long anterior process and short or adentate posterior process.

Description. The Pa element is segminiscaphate with a single row of up to 12 denticles and one cusp extending from the anterior 'blade' to a posterior expansion loosely called a 'platform'. In plan view the element is bowed slightly outward and the cusp and posterior-most denticles are twisted slightly inward. The element is differentiated into a free blade and a platform at the point where the basal margin of the element flares abruptly outward. The blade supports up to 6 denticles and there may be as many as 6 (Fig. 27H) on the platform. Specimens illustrated by van den Boogaard (1987) have as many as 13 denticles, 6 on the free blade and 7 on the platform The element is deeply excavated but the aboral view (Fig. 27A) shows that the denticulate ridge does not become appreciably wider on the platform, but that the basal margin flares outward giving the appearance of a platform. Based on specimens illustrated by van den Boogaard (1987), the outer margin of the element is broadly rounded

Fig. 29. Vjalovognathus sp. nov. A, Pa element. All views ×100, except as noted. A–K, left element (CPC 34693) [CB 03/05]: A, outer lateral view; B, inner lateral view; C, oral view; D, aboral view; E, oblique oral-anterior view; F, oblique aboral view; G, posterior-oral view; H, anterior view; I, enlargement (×470) of first blade denticle (anterior to left); J, enlargement (×470) of second blade denticle; K, enlargement (×470) of fourth and fifth blade denticles. Note on denticle enlargements the keel developed on the posterior margin of the denticle that as the denticle tip becomes more truncated accentuates the ovate to diamond shape of the denticle section.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at the basal margin of the posterior end. However, the denticle row on the oral margin tapers (Figs 11D, 27B) gradually to the cusp. The cusp is long and pointed, projecting posteriorly upward at an angle of about 45° from the plane of the eroded oral surfaces of the denticle row and extends slightly above the level of the denticles. The oral surface of the element is smooth. The denticle pattern of the element changes from the anterior to the posterior ends of the element. The anterior denticles are round to ovate with only a small anterior groove on the denticle (Fig. 27D). Progressively the denticles become more closely spaced and the groove becomes larger. On the platform the posterior-most denticles become rounded and both shorter and smaller in diameter (Fig. 11D). In cross-section the blade is narrow at the basal margin and expands laterally and then narrows to a pointed tip (Fig. 28D). Progressively toward the posterior part of the element the tips of all denticles become eroded and typically only the anterior one or two denticles are preserved to their full height.

The Pb element is anguliscaphate with a relatively long anterior process that is bent inward and supports two or more denticles. The posterior process, if present, is broken and no denticle is apparent. The denticle cross-section shape is biconvex and symmetrical. However, the cusp is asymmetrically biconvex in section view (Fig. 28M) with a relatively flattened inner face and a strongly bowed outer face. This same morphology is also reflected in the basal outline of the element with a broad outwardly protruding flange on the outer face of the element. The cusp tapers upward to a slightly rounded apex.

Remarks. Van den Boogaard (1987) illustrated 6 Pa elements which he assigned to *Vjalovognathus shindyensis*, but most of his illustrated specimens have denticles with a narrow and shallow groove centrally located on the medial anterior margin of the denticles. Reimers (1991) also illustrated two elements that he assigned to *V. shindyensis*, but which have oral-surface denticles that show that the elements should be assigned to *V. australis*. In contrast, specimens from the Canning Basin that we assign to *V. shindyensis*, and material illustrated by Kozur (1978; Fig. 11A, B), have a well developed groove on the anterior margin of the denticles and the denticles of the middle part of the element are nested. The van den Boogaard (1987) and Reimers (1991) material is thus assigned to *V. australis* and has been a valuable tool in helping to understand the morphology of the species.

Only the Pa and Pb elements of *V. australis* have been thus far recognised in samples from the Callytharra Formation. Most of the Pa elements are represented by broken portions of the central or posterior part of the platform. Only two elements are reasonably well preserved and have the posteriorly located cusp. Thus we assign the specimens illustrated by van den Boogaard (1987) and Reimers (1991) to the new species *V. australis*.

Age range. Late Sakmarian–Early Artinskian, *Mesogondolella bisselli–Sweetognathus inornatus* Zone.

Stratigraphic recovery. Southern Carnarvon Basin, Callytharra Formation; Timor, Maubisse Formation.

Vjalovognathus sp. nov. A

Figs 9G–H, 29, 30

Material studied. 4 elements (3 Pa, 1 Sc).

Diagnosis. A species of *Vjalovognathus* in which the segminiscaphate Pa element has denticles with an ovate to diamond-shaped cross-section, a prominent axial ridge running along the axial crest of the element and a short, rounded and posteriorly inclined cusp. The Sc element is bipennate with an enlarged basal cavity. Other element types have not been observed.

Description. The Pa element is segminiscaphate with at least 7 denticles and a posterior cusp on the best preserved specimen. The denticles are ovate to diamond-shaped in cross-sectional view. In lateral view the anterior denticles are discrete, but over the platform the base of the denticles appear appressed. The denticles have a well developed to prominent axial ridge running along the crest of the element that appears to start with the anterior-most denticle, but which does not extend to the cusp. The cusp is short, posteriorly inclined and round in section view. The anterior blade supports at least three denticles. The base of the thin-walled element crown is deeply excavated. The posterior margin of the base appears to be gently rounded, but our material is broken on both lateral basal margins. The basal margin tapers to have subparallel edges in the blade region. The morphology of the attachment cone is unknown. Speculatively, we suspect the attachment cone will be similar to those in well preserved specimens of *Icriodus* (Nicoll 1982).

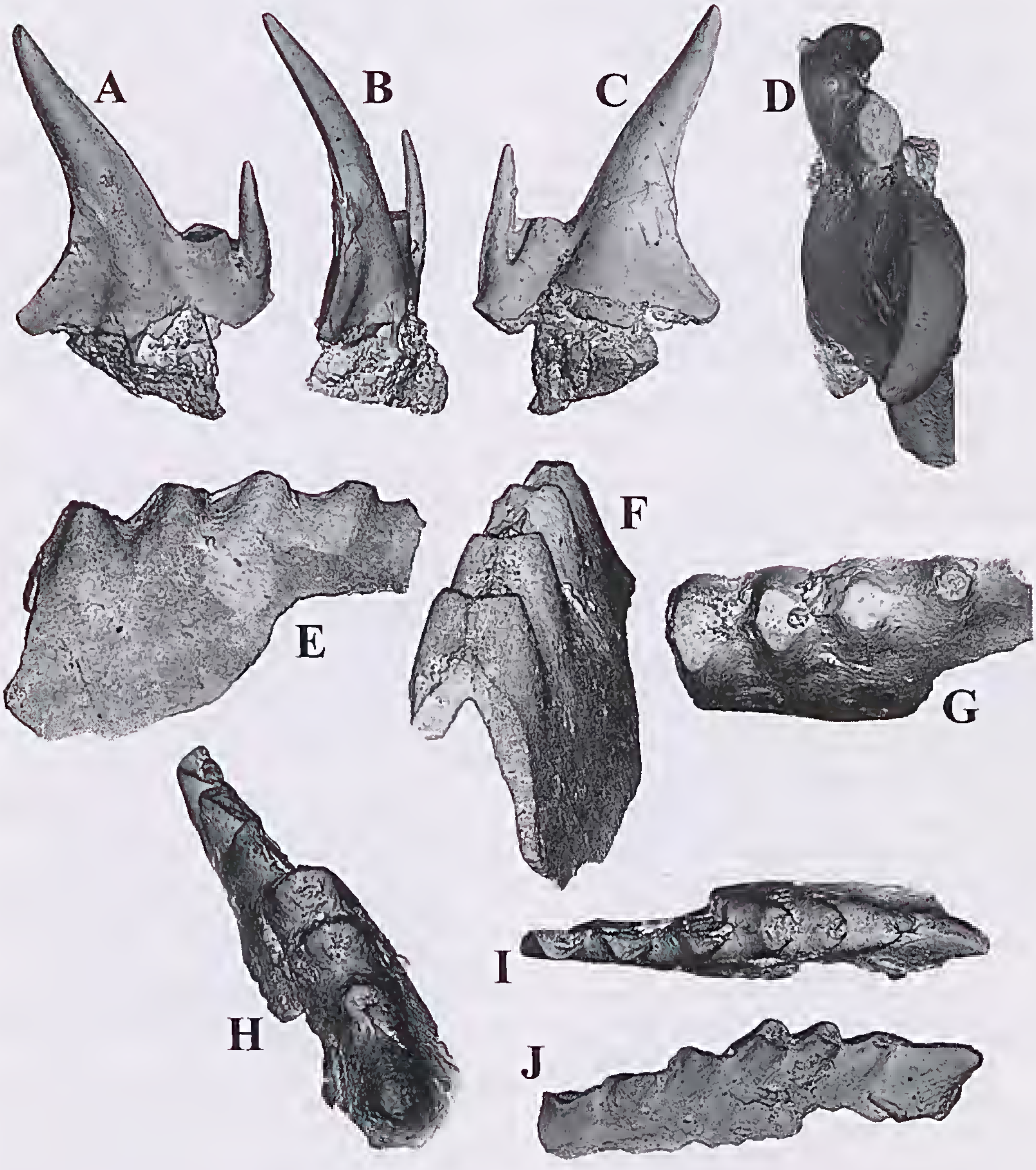

Fig. 30. Vjalovognathus sp. nov. A, Sc and Pa elements. All views ×135, except as noted. A–D, Sc element (CPC 34694) [GSWA 144101] right element: A, outer lateral view; B, posterior view; C, inner lateral view; D, enlargement (×250) of oral view showing cusp curvature and cross-section. E–G, broken left Pa element (CPC 34695) [CB 32/07]: E, outer lateral view; F, oblique anterior-outer lateral view; G, oral view (posterior to right). H–J, right Pa element (CPC 34696) [GSWA 32/7]: H, oblique oral-inner lateral view; I, oral view; J, inner lateral view.

The Se element is bipennate with a short adentate posterior process and two preserved denticles on the broken anterior process.

Remarks. Based on the limited material available this species of *Vjalovognathus* appears to be morphologically distinctive. Some elements of *V. shindyensis* show hints of an axial ridge, but it is now well developed. The anterior groove shown on most denticles of both *V. shindyensis* and *V. australis* appears to be missing. Typical of all species of *Vjalovognathus*, the apparently biologically induced truncation of the denticles produces a worn denticle cross-section that may appear diamond-shaped where the axial ridge is well developed (see Figs 29K, 30G). Where the denticle is not worn, the cross-section is essentially round except for the axial ridge (Fig. 29H, J).

Age range. ?Late Kungurian to Roadian; ?*Mesogondolella nankingensis* Zone.

Stratigraphic recovery. Southern Carnarvon Basin-Wandagee Formation, Coolkilya Sandstone.

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Appendix. Conodont locality details.

PERMIAN CONODONT COLLECTING LOCALITIES OF THE SOUTHERN CARNARVON BASIN

The following is the list of Permian outcrops sampled by Robert S. Nicoll in 1974 from Permian outcrops in the Southern Carnarvon Basin. All samples were examined in 1974, but in a review of the material in 1996 not all of the heavy residues have been located. A missing residue designation indicates that this sample was not re-picked in 1996. Please note that numerous broken fragments of *Vjalovognathus* were missed in the original 1974 picking, along with a few elements of *Hindeodus*. It is probable that the missing sample residues from Callytharra Formation section 04 will contain a number of conodont elements.

In addition to those localities listed below, samples were obtained from the Bulgadoo Shale, Thambrong Formation, Norton Greywacke and the Cundlego Formation. No conodonts were recovered from any of these units.

01 Callytharra Formation (measured section)
plotted map: Gooch Range 1:100 000 — lat./long. 23°50.81′S,114°49.46′E
remarks: section 2 of Condon (1967), southern Gooch Range, vicinity of trig point K-55, just south of the type section of the Moogooloo Sandstone (see Condon 1967: fig. 72)
29 samples: 7 productive, 1 missing residue
conodonts in samples 01/ 09, 12, 19, 26, 27, 29, 33
total weight: 84 kg — total elements: 15

02 Callytharra Formation (measured section)
plotted map: Mount Sandiman 1:100 000 — lat./long. 24°01′S,115°01′E
remarks: section not accurately located. Section just south of Minilya River, vicinity of Condon (1967) section 3, near Donollys Well.
61 samples: 18 productive, 4 missing residues
conodonts in samples 02/ 04, 07, 10, 21, 24, A44, A49, 87, 103, 104, 107, 109, 127, 154, 158, 160, 161
total weight: 171 kg — total elements: 47

03 Wandagee Formation (called Callytharra Formation) (spot samples)
plotted map: Barrabiddy 1:100 000 — lat./long. 23°45′S,114°24′E
remarks: see Condon (1967: 163, fig. 126 [map]). Study indicates this outcrop is not the Callytharra Formation as mapped by Condon (1967). Spot samples from poor exposure.
5 samples: 1 productive, 1 missing residue
conodonts in samples 03/ 05
total weight: 12 kg — total elements: 7

04 Callytharra Formation (measured section)
plotted map: Winning 1:100 000 — lat./long. 23°20.82′S,114°40.59′E to 23°20.82′S,114°40′E
remarks: section 1 of Condon (1967), just south of the Lyndon River (see Condon 1967: fig. 68)
90 samples: 3 productive (this section not re-picked, would expect more elements to be recovered), 90 missing residues
conodonts in samples 04/ 11, 15, 97
total weight: 270 kg — total elements: 4

05 Callytharra Formation (measured section)
plotted map: Yalbalgo 1:100 000 — lat./long. 25°02.15′S,114°58.58′E
remarks: type section Jimba Jimba Calcarenite of Condon, now recognised as the upper part of the Callytharra Formation (Mory 1997, pers. comm.)
38 samples: 3 productive, 2 missing residues
conodonts in samples 05/ 01, 08, 10
total weight: 114 kg — total elements: 7

06 Callytharra Formation (measured seetion)
plotted map: Daurie Creek 1:100 000 orthophoto map lat./long. 25°13.5′S,115°32′E to 25°13.0′S,115°31′E
remarks: seetion 7, Pells Range, of Condon (1967), middle-upper part of seetion very poorly exposed and not collected exeept for samples at top
39 samples: 7 productive, 2 missing residues
eonodonts in samples 06/ 02, 04, 05, 09, 19, 21, 29
total weight: 111 kg total elements: 8

20 Callytharra Formation (lower part)
plotted map: Yalbalgo 1:100 000 lat./long. 25°02′S,114°58.64′E
remarks: Jimba Jimba Syncline area, south of the Gascoyne River. Portion of Callytharra Formation below the sandstone member. Probably approximated section 8 of Condon (1967). See Condon (1967: figs 64 [map], 65, 76).
15 samples: 4 productive, 1 missing residue
eonodonts in samples 20/ 01, 02, 04, 11
total weight: 40.8 kg total elements: 14

22 Callytharra Formation (lower part)
plotted map: Yalbalgo 1:100 000 lat./long. 25°02.78′S,114°59.00′E
remarks: spot sample in test pit of Public Works Dept (WA), probably equivalent to upper shale interval of section 20 (see seetion 20 above)
1 sample: 1 produetive.
conodonts in samples 22/ 01
total weight: 25 kg total elements: 5

32 Coolkilya Greywacke
plotted map: Mardathuna 1:100 000 lat./long. 24°7.32′S,114°50′E
remarks: vieinity of Southern Cross Bore, near reference seetion of Condon (1967: 183, figs 139, 140)
7 samples: 1 productive
conodonts in samples 32/ 07b
total weight: 27 kg total elements: 1

34 Coyrie Formation
plotted map: Mount Sandiman 1:100 000 lat./long. 24°5.08′S,115°7.23′E
remarks: type section, see Condon (1967: 126, figs 78 [map], 102 [section])
2 samples:
conodonts in samples 34/ 01
total weight: 3 kg total elements: 1

36 Coyrie Formation
plotted map: Winning 1:100 000 lat./long. 23°23.66′S,114°32.76′E
remarks: colleeted along Lyndon River, NE of track from Five Mile Bore to vicinity of Charly Well. Spot samples.
3 samples: 1 produetive
eonodonts in samples 36/ 02
total weight: 9 kg total elements: 1

41 Coyrie Formation
plotted map: Yalbalgo 1:100 000 lat./long. 25°11.17′S,114°59.82′E
remarks: spot sample of float near outerop, south of Boolardy Well
1 sample: 1 produetive
conodonts in samples 41/ 01
total weight: 3 kg total elements: 4